LINKING ENERGY BALANCE TO SURVIVAL IN MULE DEER: DEVELOPMENT AND TEST OF A SIMULATION MODEL

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Abstract: I developed a model of energy balance in mule deer (*Odocoileus hemionus*) that predicts changes in body size and fatness of the average doe and fawn and predicts rates of mortality due to starvation in populations of does and fawns. Model predictions respond to input on the amount, quality, and structure of forage, the density of deer, and daily weather conditions (max. and min. temp. and snow depth). Application of the model is restricted to shrub–steppe and shrub–woodland ranges. Energy expenditure is simulated as the sum of hourly costs of activity (posture, locomotion, eating), resting (lying, ruminating), and thermoregulation. Daily snow depth and characteristics of forage influence energy intake. Differences between energy intake and expenditure are related to a normal distribution of energy reserves that is used to predict mortality rate. Model predictions of overwinter mortality in does and fawns closely resembled trends in field measurements of mortality during 14 different years in 2 different habitats. Model predictions of fat reserves did not differ from measured values during early and midwinter, but diverged from measurements at winter's end. Weather during a severe winter increased simulated energy expenditure by 4% (10,019 vs. 9,621 kcal/kg$^{0.75}$/winter) in does and 2% (10,879 vs. 10,632 kcal/kg$^{0.75}$/winter) in fawns relative to their expenditures during a mild winter, and reduced intake of metabolizable energy by 17% in both does (133,183 vs. 161,292 kcal/winter) and fawns (94,663 vs. 114,643 kcal/winter). Predictions of mortality were more responsive to changes in snow depth than to changes in temperature. Simulated mortality declined sharply in response to increases in parameter values for digestibility of winter forage, forage intake rate, supplemental feed offered, and fatness of animals during autumn. Reducing deer density and increasing forage amount influenced mortality only when prewinter forage was scarce (<150 kg/ha) or when there was a high variance in the quality or availability of food. Enhancing thermal cover had negligible effects on simulated mortality. By organizing results of nutritional research in a form that is accessible and interactive, the model can facilitate decisions on managing mule deer populations and their habitats.

CONTENTS

INTRODUCTION

Recent advances in understanding processes controlling energy intake, assimilation, storage, and expenditure in mule deer offer a basis for predicting their energy balance at a higher level of realism than has been possible before (Parker and Robbins 1984; Parker et al. 1984; Wickstrom et al. 1984; Torbit et al. 1985*a,b*, 1988; Spalinger et al. 1986; Baker and Hobbs 1987). Such predictions depend on constructing a model simulating the influence of the environment on the animal's energy gains and losses.

A simulation model of energy balance in mule deer assembles knowledge in a form particularly useful to wildlife managers and researchers. Although studies of animal energetics can enhance decisions on managing mule deer populations and their habitats (e.g., Parker and Robbins 1984:486), much of this information remains inaccessible to decision makers. This is the case because the focused studies that are essential to understanding singular as-

pects of deer energetics cannot be expected to predict the multiple responses of the whole animal or the implications of those responses for deer populations. However, wildlife managers must choose among actions affecting populations rather than those affecting a single deer. Consequently, models linking processes in individual animals with processes in animal populations are urgently needed. Assembled in a validated model, studies of deer energetics can collectively influence management decisions in ways they have not achieved individually.

A model also is needed by researchers. Rapid progress in understanding physiological processes in mule deer threatens to surpass our understanding of the ecological significance of those processes. Collecting the results of reductionist studies in a model that responds to environmental variables will place findings on deer physiology in their proper ecological context. Moreover, planning effective research de-

pends on identifying influential but poorly understood elements of past findings. By assessing the relative importance of variables and processes, a model can illuminate worthwhile objectives for future investigation. Finally, there are many questions in deer ecology, particularly questions operating at the ecosystem level, that are not amenable to traditional, designed experiments (Romesburg 1981, Hurlbert 1984). Such experiments demand environmental manipulation on a scale that is simply too costly to impose. For example, it is plausible that the effect of deer density on population mortality rates depends on the biomass of forage available to those populations. However, the nature of this interaction remains undescribed, and a replicated, factorial experiment simultaneously varying population density and food supply is probably not soon forthcoming. Developing adequately predictive models may offer the only feasible way to address such otherwise intractable problems.

Here, I describe a model of energy balance in mule deer during winter. The model was built to predict changes in body condition of the average mule deer doe and fawn and to predict the relationship of those changes to rates of mortality in populations of does and fawns. In so doing, I wanted the model to illuminate the relative importance of processes of energy loss and gain in mule deer. I also developed the model to provide a gaming tool for addressing ecosystem-level questions on interactions between mule deer populations and the habitats they use. I used this tool to evaluate the ability of prevalent management practices to reduce starvation in mule deer populations during winter.

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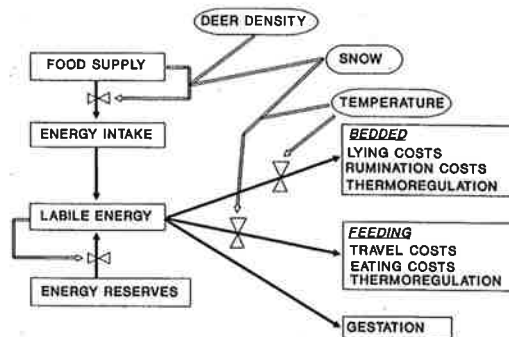

Fig. 1. Simplified schematic of model structure. Variables in boxes are calculated within the model. Variables in ellipses are input by the user. Solid lines show transfer of energy. Clear lines illustrate control of processes.

METHODS
Model Boundaries

The model operates within distinct spatial and temporal boundaries. Spatially, the model simulates mule deer on shrub–steppe and shrub–woodland ranges of the central Rocky Mountains. Its predictions are limited to areas where starvation is the major cause of winter mortality or is compensatory with other causes. In a strict sense, the model operates within the confines of an "average" doe or fawn and extrapolates from its behavior to the behavior of a normally distributed population of does or fawns. The model is bounded in time by the beginning and end of plant senescence, and applies only to months of the year when plants are predominantly dormant.

Model Structure and Implementation

The structure of the model follows the conceptual approach of Wunder (1978). The model simulates energy flow from forage resources to the animal and the allocation of that energy to individual expenditures by the animal (Fig. 1). When the sum of energy expenditures exceeds energy gains, the animal's endogenous reserves of energy are reduced to offset those deficits. State variables include the calories of metabolizable energy in the forage stand-

Table 1. Glossary of principal parameters in simulation model of energy balance in mule deer.

Name	Type[a]	Definition	Units	Initial value[b]	Reference
AMIN	var	Time spent active	min	0.0	
ATR	var	Cost of thermoregulation in active state	kcal/min	0.0	
BAL	var	Daily energy balance	kcal	0.0	
BMIN	var	Time spent bedded	min	0.0	
BH	cons	Doe brisket height	cm	57.1	Parker et al. 1984
BH	cons	Fawn brisket height	cm	48.4	
BW	var	Doe daily body mass	kg	60.0, 65.0	Torbit et al. 1988
BW	var	Fawn daily body mass	kg	25.0, 30.0	Torbit et al. 1988
BW_{in}	cons	Doe prewinter body mass	kg	60.0, 65.0	Torbit et al. 1988
BW_{in}	cons	Fawn prewinter body mass	kg	25.0, 30.0	Torbit et al. 1988
CHEWMAX	cons	Maximum instantaneous rate of intake	g/min	37.6	Wickstrom et al. 1984
DMI	var	Instantaneous rate of dry matter intake	g/min	0.0	
DMICO	cons	Maximum rate of daily intake for does	% of BW_{in}	1.7	Baker and Hobbs 1987
DMICO	cons	Maximum rate of daily intake for fawns	% of BW_{in}	2.9	Alldredge et al. 1974
DIG	var	Digestibility of gross energy in grass–browse diet	unitless	0.38	Baker and Hobbs 1987
DKM	var	Distance traveled	km	0.0	
EA	var	Cost of active state	kcal	0.0	
EBAL	var	Size of energy reserves needed to survive winter	kcal	0.0	
EEAT	var	Net cost of eating	kcal	0.0	
EI	var	Metabolizable energy intake	kcal	0.0	
EL	var	Costs of bedded state	kcal	0.0	
ES	var	Costs of posture in the active state	kcal	0.0	
ET	var	Net cost of travel	kcal	0.0	
ELTR	var	Thermoregulation cost of lying animal	kcal/min	0.0	
FATPER	cons	% of body mass as fat in does, prewinter	unitless	0.11, 0.13	Torbit et al. 1988
FATPER	cons	% of body mass as fat in fawns, prewinter	unitless	0.05, 0.08	Torbit et al. 1988
GEST	var	Costs of gestation	kcal	0.0	Carpenter et al. 1979
HERB	var	Proportion of herbs (grasses + forbs) in diet	unitless	0.80	Milchunas et al. 1978
HRBDIG	cons	Digestibility of herbs	unitless	0.40	Hobbs et al. 1983
HRBMASS	var	Biomass of herbs	kg/ha	200.0	Hobbs and Spowart 1984
HRBHT	cons	Height of the herb layer	cm	30.0	Carpenter et al. 1980
HERBIN	cons	Initial conditions for herbs in diet	unitless	0.80	Carpenter et al. 1979
LCT_a	var	Lower critical temperature of active animal	C	0.0	
LCT	cons	Lower critical temperature of bedded animal	C	−22.0	Parker and Robbins 1984
LYCOST	cons	Energy cost of lying in thermoneutrality	kcal/min	0.0	
ME	cons	Metabolizability of digestible energy	unitless	0.82	Robbins 1983: Table 13.8
OBJ	cons	Hourly objective for dry matter intake	g	0.0	
PERGEST	var	Elapsed proportion of gestation period	unitless	0.0	

Name	Type[a]	Definition	Units	Initial value[b]	Reference
LYCOST	cons	Energy cost of lying in thermoneutrality	kcal/min	0.0	
ME	cons	Metabolizability of digestible energy	unitless	0.82	
OBJ	cons	Hourly objective for dry matter intake	g	0.0	
PERGEST	var	Elapsed proportion of gestation period	unitless	0.0	Robbins 1983: Table 13.8

Table 1. Continued.

Name	Type[a]	Definition	Units	Initial value[b]	Reference
RATEIN	cons	Rate constant for functional response	unitless	33.5	Wickstrom et al. 1984
RES	cons	Labile energy reserve	kcal	0.0	
RESCV	cons	Coefficient of variation on % body fat in does	unitless	0.21	Torbit et al. 1988
RCV	cons	Coefficient of variation on body fat in fawns	unitless	0.45	Torbit et al. 1988
RMUL	cons	Proportion of active time spent traveling in untracked snow for does	unitless	0.50	
RMUL	cons	Proportion of active time spent traveling in untracked snow for fawns	unitless	0.25	
RSD	var	Relative sinking depth	unitless	0.0	
RUM	var	Cost of rumination in does	kcal/min	0.085	Fancy and White 1985a
RUM	var	Cost of rumination in fawns	kcal/min	0.012	Fancy and White 1985a
RUMTIME	var	Hourly rumination time[c]	min	26.7	
SD	var	Snow depth	cm	input	
SHRUB	var	Proportion of shrubs (stems + evergreen leaves) in diet	unitless	0.20	Carpenter et al. 1979 Milchunas et al. 1978 Hobbs et al 1983
SHRBDIG	cons	Digestibility of shrubs	unitless	0.30	Hobbs and Spowart 1984
SHBMASS	var	Biomasss of shrubs	kg/ha	500.0	Carpenter et al. 1980
SHBHT	cons	Height of shrubs	cm	100.0, 80.0	
SNO	var	Relative increase in net cost of travel due to snow	unitless	0.0	
STANDCO	cons	Energy cost of standing in thermoneutrality for does	$kcal/kg^{0.75}/min$	0.0627	Parker and Robbins 1984
STANDCO	cons	Energy cost of standing in thermoneutrality for fawns	$kcal/kg^{0.75}/min$	0.0750	Parker and Robbins 1984
T	var	Hourly temperature	C	0.0	
TMAX	var	Daily maximum temperature	C	input	
TMIN	var	Daily minimum temperature	C	input	
TC_a	cons	Thermal conductance of standing animal	$kcal/kg^{0.75}/min/C$	0.004	Parker and Robbins 1984
TC_l[d]	cons	Thermal conductance of lying animal	$kcal/kg^{0.75}/min/C$	0.0027	Parker and Robbins 1984
TOTIN	var	Daily intake of metabolizable energy	kcal	0.0	
TOTOUT	var	Daily expenditure of energy	kcai	0.0	
WTBAL	var	Daily change in weight	g	0.0	
ZBAL	var	Standard normal variate for energy reserves	unitless	0.0	
ZINTAKE	var	Realized hourly intake of dry matter	g	0.0	

[a] var = variable, cons = constant.
[b] Values of variables with initial conditions = 0.0 are calculated internally during the first hour of the simulation. When 2 values are given, the first value (leftmost) is for Piceance simulations; the second is for Middle Park simulations.
[c] During 18 hours of day when feeding is not at peak. Runtime = 0.0 during peak feeding.
[d] Assuming that $TC_l = TC_a \cdot 0.67$.

ing crop, the labile energy pool in the animal, and the animal's endogenous energy reserves. Rates of flow from these variables respond to changes in operative temperature, snow depth, and animal density.

The model is structured as a series of difference equations and operates at an hourly time step. It is programmed in FORTRAN 77 (Microsoft version 4.01) for execution on IBM-compatible microcomputers. Many of the initial conditions and constants in the model can be easily modified by the user. I constructed the model to make it accessible to persons with minimal experience with computer simulations. (*See* Appendix for a user's guide and instructions on obtaining the program.)

Model Formulation

Energy Intake and Activity Budget.— The model is formulated such that energy intake is closely coupled with the animal's activity budget. (*See* Table 1 for a glossary of model variables.) Voluntary intake of dry matter is controlled on 2 temporal scales. I presume that gut fill limits daily intake of dry matter (Ammann et al. 1973, Spalinger et al. 1986, Baker and Hobbs 1987) and that forage availability regulates instantaneous intake in a threshold fashion (Wickstrom et al. 1984, Hudson and Watkins 1986, Renecker and Hudson 1986, but also *see* Spalinger et al. 1988). It follows from this premise that feeding time increases when availability of food is sufficiently reduced to cause instantaneous intake rate to decline, but that daily intake will remain unchanged until feeding time becomes constrained. Thus, the animal compensates for declining food availability by spending more time feeding in an attempt to obtain its maximum possible daily intake, which is determined by gut fill. The extent to which the animal can achieve that compensation is limited by rumination time and by the energy costs of activity.

Specifically, maximum daily intake is set at 1.7% of the initial body mass (BW_{in}, in kg) of adult does (Alldredge et al. 1974, Baker and Hobbs 1987) and at 2.9% of the body mass of fawns (Alldredge et al. 1974).

I assume that total daily intake is not influenced by diet composition (Baker and Hobbs 1987:fig. 1C). This represents a departure from previous models (Swift 1983, Hudson and White 1985*a*) where intake was controlled by dietary characteristics. However, Baker and Hobbs (1987:fig. 1G) found that deer could expand gut fill to compensate for slowly excreted forages, thereby maintaining relatively constant dry matter intake in the face of marked changes in their diets. Moreover, rumen turnover, and hence intake, is relatively insensitive to differences in physical characteristics of diets when dietary cell-wall levels exceed about 40% of dry matter, or when lignin exceeds 5% of dry matter (Spalinger et al. 1986:figs. 4, 6). This is frequently the case for winter forages, particularly for mature grasses and woody browse (Milchunas et al. 1978:table 4). Thus, the assumption of a constant limit on intake will be reasonable when deer diets are dominated by senescent grass and stems of shrubs (e.g., Carpenter et al. 1979), but may underestimate potential daily intake when diets contain a substantial portion of forbs or shrub leaves with thin cell walls (Spalinger et al. 1986).

Potential daily intake is represented as a function of initial body weight. Realized food intake is calculated as the sum of hourly intake as it is modified by feeding behavior. Hourly intake is determined by eating rate and feeding time. Eating rate is estimated as a function of biomass of selected food using the equations of Wickstrom et al. (1984:fig. 1). Because these equations did not extend to low levels of biomass for mixed shrub–herb communities, I developed a relationship between biomass and intake as follows. Maximum eating rate was set at 3.76 g/minute (Wickstrom et al. 1984). I assumed that eating rate declines when available food biomass falls below 50 kg/ha (as it does in grasslands, Wickstrom et al. 1984:fig. 1). I changed the denominator in a Mechalis-Menton equation to achieve an asymptote at about 50 kg/ha. This produced a rate constant where the instantaneous rate of intake was half its maximum value at food biomass equal to 33.5 kg/ha:

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$$DMI = [CHEWMAX \cdot (HRBMASS + SHBMASS)] \div (RATEIN + HRBMASS + SHBMASS)$$

where

DMI = instantaneous rate of dry matter intake (g/min),

$CHEWMAX$ = maximum instantaneous intake rate (=3.76 g/min),

$HRBMASS$ = biomass of selected herbs (kg/ha),

$SHBMASS$ = biomass of selected shrubs (kg/ha), and

$RATEIN$ = rate constant (=33.5).

Thus, instantaneous eating rate by the animal is controlled by the available biomass of herbs and shrubs in the plant community being modeled.

Food biomass is determined by the initial supply of herbs and shrubs and is modified by snow depth and daily forage removal by the deer population. The user enters data on the biomass (kg/ha) of herbs and shrubs present at the beginning of winter, as well as information on the structure of their standing crops. Required structural information includes an approximation of the average height of the herb and shrub layers in the plant community. This information is input by the user for the plant community being modeled.

Increasing snow depth causes linear reductions in food supply. I assume that the availability of herbs (HRBAV in kg/ha) is proportional to snow depth; herb biomass begins to decrease in availability when snow depth is > 0 and diminishes until herbs become completely unavailable when snow depth exceeds the height of the herb layer:

$$HRBAV = HRBMASS - [SD \cdot (HRBMASS \div HRBHT)]$$

where

$HRBMASS$ = biomass of herbs,

SD = snow depth (cm), and

$HRBHT$ = average height of the herb layer (cm).

Availability of shrubs is modeled similarly. This is a simplification of reality and does not incorporate effects of changes in characteristics of the snow surface (crusting, slabbing) or behavioral response of deer (pawing). Although the influence of snow accumulation on availability of forage to deer remains poorly described, there is evidence (Gilbert et al. 1970, Carpenter et al. 1979, Sweeney and Sweeney 1984, Adamczewski et al. 1988) that the above formulation, although simple, represents this influence in a reasonable way.

The animal's "objective" for hourly intake is controlled by the maximum intake allowable each day. This hourly objective, in turn, is used to calculate feeding time. During each hour the animal divides its time between 2 states—feeding (AMIN, in min) and bedded (BMIN, in min):

$$AMIN + BMIN = 60.0$$

Feeding time expands to allow the animal to approach or meet its objective for dry matter intake during each hour (OBJ_{thr}, in g). That goal is calculated from the potential daily intake. I assume that feeding time is spaced continuously throughout the day and night with peaks occurring during early morning and evening (Miller 1970, Carpenter 1976, Eberhardt et al. 1984). Thus, deer feeding behavior is represented such that 30% of daily intake occurs during 0600–0800 hours, 30% during 1800–2000 hours, and the remaining 40% during the rest of the day and night. For example, assuming that daily intake of the average doe can be estimated as 1.7% of her initial body weight (BW_{in}, in kg) (Alldredge et al. 1974, Baker and Hobbs 1987), her "goal" for hourly intake during 0700 hour is

$$OBJ_{0700} = [(BW_{in} \cdot 0.017) \cdot 0.30] \div 3.0.$$

The animal feeds long enough each hour to obtain its intake goal (OBJ_{thr}),

$$AMIN = OBJ_{thr} \div DMI;$$

and is bedded (BMIN) for the remainder of the hour,

$$BMIN = 60.0 - AMIN.$$

However, the duration of feeding each hour is limited by rumination time (RUMTIME, in min) required for the food eaten. I assume that the animal ruminates for 8 hours a day and that rumination occurs while the animal is bedded during hours other than those of peak feeding. When feeding is not at its peak, bedded time (BMIN) cannot fall below RUMTIME, and hourly feeding time (AMIN) cannot exceed it. Given these constraints on AMIN, the realized hourly dry matter intake (ZINTAKE, in g) is

$$ZINTAKE = DMI \cdot AMIN$$

where

$$AMIN \leq (60.0 - RUMTIME).$$

Hourly intake of metabolizable energy (EI, in kcal) is calculated as the product of the realized dry matter intake and forage gross energy (4.2 kcal/g, Golley 1961, Milchunas et al. 1978) multiplied by appropriate coefficients as follows:

$$EI = ZINTAKE \cdot 4.2 \cdot ME \cdot DIG$$

where

ME = 0.82 kcal metabolized/kcal digested (Robbins 1983:table 13.8) and

DIG = kcal digested/kcal gross (calculated below).

I do not include a coefficient of net energy in this calculation because energy requirements are formulated to include heat increment (i.e., measurements were made on fed animals, Parker and Robbins 1984). Thus, because the summed energy requirements of the animals implicitly include the cost of heat increment, the summed energy intake should include energy that can be used to offset that cost. If requirements were based on fasted animals, then those requirements would not reflect calories expended in work of digestion, rumen fermentation, etc. Such calories should be excluded from energy intake (using a net energy coefficient) only when they cannot meaningfully offset a component of the animal's summed energy requirements. My approach resembles that of Fancy (1986), except that I do not ex-

plicitly account for dietary influences on heat increment.

The digestibility of dietary energy is influenced by the composition of the dietary dry matter, which is determined by the availability of herbs and shrubs as it is modified by snow depth. I assume that the composition of deer diets is not influenced by snow depth (SD, in cm) until accumulated snow exceeds 10 cm. Above that point, the proportion of herbs in the diet dry matter (HERB, a decimal fraction) decreases in proportion to increasing snow depth (Carpenter et al. 1979:fig. 3) until the diet is composed entirely of shrubs when snow depth exceeds the height of the herb layer. Thus,

$$HERB = HERBIN - \{(SD - 10.0) \cdot [HERBIN \div (HRBHT - 10.0)]\},$$

but if SD > HRBHT, then HERB = 0

where

HERBIN = initial condition for % herbs in diet,

SD = snow depth, and

HRBHT = average height of the herb layer.

The digestibility of the diet (DIG, in kcal digested energy/kcal gross energy) is then calculated as the average of the digestibilities of herbs (HRBDIG) and shrubs (SHRBDIG) weighted by their calculated percentage in the diet as follows:

$$DIG = (HERB \cdot HRBDIG) + (SHRUB \cdot SHRBDIG).$$

If the animal's energy costs of feeding during any hour exceed the energy it could gain by feeding during that hour, then I assume the animal beds rather than feeds (AMIN = 0, BMIN = 60); I set dry matter intake to 0, and I add the dry matter the animal would have obtained during that hour to the intake goal for the remaining hours of the day. There is no carryover in the intake goal between days.

At the end of each day, I reduce the supply of herbs and shrubs by the amount consumed by the animal multiplied by the density of deer in the habitat weighted by

the sex and age composition of the population. Thus, although the model simulates a doe or fawn, forage removal reflects the collective effects of a population of does, bucks, and fawns. It follows that changes in forage biomass and deer density have parallel effects on forage availability; each influences the amount of forage available per animal in the population.

Energy Expenditure.—Energy costs incurred by the animal are influenced by daily snow depth and hourly temperature. The user enters values for daily snow depth and maximum and minimum air temperatures. Hourly temperatures are estimated from daily maximum and minimum temperatures following the algorithm of Parton and Logan (1981). Energy costs are summed over the time the animal spends in the 2 possible behavioral states—active and bedded. Bedded energy costs are formulated as the sum of costs of lying, rumination, and thermoregulation.

The cost of lying in a thermoneutral environment (LYCOST, in kcal/min) is calculated as a function of the standing cost:

$$\text{LYCOST} = (\text{STANDCO} \div 1.33) \cdot \text{BW}^{0.75}$$

where STANDCO = 0.0627 kcal/min/$\text{kg}^{0.75}$ for does and 0.075 kcal/min/$\text{kg}^{0.75}$ for fawns. (The value for fawns represents a weighted average for the winter to account for changes in STANDCO as the animal matures.) This formulation is based on the data of Parker and Robbins (1984: fig. 12) on standing costs, assuming that energy expenditure is 33% higher for standing than for lying (mean of 9 studies of wild ruminants: Maloiy 1968, Wesley et al. 1973, Renecker and Hudson 1978, White and Yousef 1978, Chappel and Hudson 1979, Gates and Hudson 1979, Mautz and Fair 1980, Parker and Robbins 1984, Fancy 1986). I assume that the animal ruminates when it is bedded and that rumination costs (RUM, in kcal/min) are 2% of lying costs (Fancy and White 1985a: 146). Therefore,

$$\text{RUM} = \text{LYCOST} \cdot 0.02.$$

Calculating the costs of thermoregulation of the lying animal is problematic be-cause the best measurements of energy costs of thermoregulation in mule deer were obtained from standing animals (Parker and Robbins 1984). I used the following approach to deal with this problem. I assumed that the thermal conductance of a lying animal (TC_l) is 67% (Gates and Hudson 1979:fig. 2) of that of a standing animal ($\text{TC}_s = 0.004$, Parker and Robbins 1984:fig. 12) and that heat production can be estimated as a linear function of temperature below the animal's lower critical temperature (Parker and Robbins 1984:fig. 12, but also *see* fig. 14). However, if thermal conductance and heat production change when the animal lies down relative to their value when the animal stands (Gates and Hudson 1979), then lower critical temperature also will change. Following the reasoning of Kleiber (1975:169), I calculated a lower critical temperature for the lying state as

$$\text{LCT}_l = \text{XIN} - (\text{LYCOST} \div \text{TC}_l)$$

where

LCT_l = lower critical temperature of bedded animal (C),

XIN = X-intercept of extrapolated line describing heat production below lower critical temperature (C),

LYCOST = heat production of bedded animal in thermoneutrality (kcal/min), and

TC_l = thermal conductance of bedded animal (kcal/$\text{kg}^{0.75}$/min/C).

Theoretically, XIN should equal the animal's core body temperature assuming that thermal conductance can be described by Newton's Law of Cooling (Kleiber 1975). In fact, the animal's core temperature exceeds XIN in several North American ungulates (Parker and Robbins 1985). However, I assume that the consistently linear relationship between heat production and operant temperature below the animal's lower critical temperature allow me to treat thermal conductance and XIN as constants (Parker and Robbins 1984:fig. 12).

Thermoregulation costs associated with the lying state (ELTR, in kcal/min) are

set at 0.0 until the hourly temperature drops below LCT_l when they are calculated as

$$ELTR = [TC_l \cdot (LCT - T)] \cdot BW^{0.75}$$

where

$ELTR$ = bedded costs of thermoregulation (kcal/min),
T = hourly temperature (C),
LCT_l = lower critical temperature of bedded animal (C), and
TC_l = thermal conductance of bedded animal (kcal/kg$^{0.75}$/min/C).

Total bedded costs (EL, in kcal) for the hour are then calculated as the sum of costs of thermoregulation, lying, and ruminating:

$$EL = [(ELTR + LYCOST) \cdot BMIN] + (RUM \cdot RUMTIME).$$

Energy costs of activity are formulated as the sum of the costs of maintaining posture (i.e., the "standing" component of travel), the net cost of locomotion as it is influenced by snow, and the net cost of eating. Posture costs (ES, in kcal) are calculated (Parker and Robbins 1984) as

$$ES = STANDCO \cdot BW^{0.75} \cdot AMIN.$$

The net cost of locomotion (ET, in kcal) is estimated as the energy needed to move a specific distance assuming the travel velocity while feeding equals 1.5 m/minute (Wickstrom et al. 1984). The distance traveled (DKM, in km) is thus

$$DKM = AMIN \cdot 1.5 \div 1,000$$

and locomotion costs (ET, in kcal) can be calculated as follows (Parker and Robbins 1984):

$$ET = 2.97 \cdot BW^{-0.34} \cdot DKM \cdot BW.$$

Following the formulation of Parker et al. (1984), the net cost of locomotion is elevated by a scalar (SNO, unitless) that represents the relative increase in energy expended to travel in snow:

$$ET = ET + (ET \cdot SNO).$$

This scalar is a function of relative sinking depth (RSD), which is calculated from snow depth (SD, in cm) and the animal's brisket height (BH, in cm):

$$RSD = (SD \div BH) \cdot 100.$$

Brisket height is calculated from the formula of Parker et al. (1984) as

$$BH = 21.0 \cdot [\ln(BW_{in} + 1.0)^{0.707}],$$

and SNO can then be calculated as

$$SNO = [0.71 \cdot RSD \cdot e^{(0.19 \cdot RSD)}] \div 100.$$

However, because mule deer are gregarious, 1 animal often follows in another's footsteps. Consequently, I reduce the effect of snow by the proportion of the animal's hourly feeding time it spends traveling in untracked snow (RMUL, unitless):

$$SNO = SNO \cdot RMUL.$$

There were no data available to estimate RMUL, so I approximated a value of 0.50 for does and 0.25 for fawns.

The energy cost of eating over standing and travel (EEAT, in kcal) is estimated from values derived from studies of elk (Wickstrom et al. 1984) as

$$EEAT = 0.0053 \cdot BW \cdot AMIN,$$

and the total cost of activity in thermoneutrality (EA, in kcal) is calculated by summing the costs of posture, travel, and eating as

$$EA = ET + ES + EEAT.$$

Thermoregulation costs of the active state (ATR, in kcal/min) are added to EA whenever the hourly operative temperature drops below the animal's lower critical temperature during activity (LTC_a, in C):

$$ATR = [0.004 \cdot (LCT_a - T)] \cdot BW^{0.75}$$
$$EA = EA + (ATR \cdot AMIN).$$

I assume that the thermal conductance for a slowly moving animal (1.5 m/min, Wickstrom et al. 1984) does not differ substantially from that for a standing animal. There is evidence that thermal conductance increases during activity (Gates and Hudson 1979). However, these data are

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difficult to interpret because the level of activity (and hence heat production) is virtually impossible to control. Consequently, differences in activity costs are confounded with differences in thermoregulation costs.

Based on the same reasoning I described above for LTC_l, I calculate a lower critical temperature for the active state as a function of heat production (EA, in kcal) and thermal conductance for a standing animal (TC_a, in kcal/kg$^{0.75}$/min/C). Thus,

$$LCT_a = [XIN - (EA \div AMIN)] \div (BW^{0.75} \div TC_a),$$

where

LCT_a = lower critical temperature of active animal (C),

XIN = X-intercept of the extrapolated line describing heat production below lower critical temperature (C),

EA = heat production of active animal in thermoneutrality (kcal), and

TC_a = thermal conductance of active animal (kcal/kg$^{0.75}$/min/C).

Energy costs of gestation (GEST, in kcal) are added daily to the sum of the hourly costs of lying and activity. Gestation costs are calculated from initial body weight and the elapsed percentage of the gestation period (PERGEST, in %) following the formulation of Robbins (1983):

$$GEST = (70 \cdot BW_{in}^{0.75}) \cdot [.000024 \cdot (PERGEST^{3.13}) \div 100].$$

I assume a 200-day gestation period and conception on 1 December.

Energy Balance, Weight Change, and Mortality.—At the end of each day, I sum the hourly values for energy intake (TOTIN, in kcal) and expenditure (TOTOUT, in kcal) and use their difference (BAL = TOTOUT − TOTIN, in kcal) to predict weight change (WTBAL, in g). Thus,

$$WTBAL = [0.70 \cdot (BAL \div 9.5)] + [0.30 \cdot 4.0 \cdot (BAL \div 4.8)]$$

where

0.70 = proportion of total calories catabolized from fat (Torbit et al. 1985b),

9.5 = kcal/g fat catabolized (Kleiber 1975:table 7.3),

0.30 = proportion of calories catabolized from protein (Torbit et al. 1985b),

4.0 = g H_2O/g protein catabolized (Torbit et al. 1985a), and

4.8 = kcal/g protein catabolized (Kleiber 1975:table 7.3).

Whenever WTBAL is > 0.0, I subtract it from the animal's body weight. This formulation requires 2 major assumptions. I assume that the ratio of calories catabolized from fat relative to those catabolized from protein is not influenced by the magnitude of energy deficits (Torbit et al. 1985b, but also *see* Owen et al. 1969). Moreover, I assume that deer will not "grow" during winter; when energy balance is ≥ 0.0, body weight does not increase. Although this is probably the case for adults, it may oversimplify the situation for fawns (Wood et al. 1962, Nordan et al. 1968, McEwan 1975, Bahnak et al. 1981). However, I felt this simplification was justified to eliminate the need to represent processes of anabolism. At the end of the winter, I sum the daily values for energy deficits to estimate the size of energy reserves needed by an animal to survive winter (EBAL, in kcal):

$$EBAL = \sum (TOTIN - TOTOUT)$$

where

TOTIN = daily metabolizable energy intake (kcal), and

TOTOUT = daily energy expenditure (kcal).

To survive, animals must be able to mobilize reserves of energy ≥ EBAL. Thus, the proportion of the population that starves to death can be estimated as the proportion of the population that began the winter with energy reserves smaller than EBAL.

I approximate this proportion as follows. I create a standard normal variate (ZBAL)

by subtracting the mean energy reserves in the population (RES) from EBAL and dividing that difference by the population standard deviation,

$$ZBAL = (EBAL - RES) \div (RES \cdot RESCV),$$

where RESCV is the coefficient of variation on energy reserves. Assuming that energy reserves in the population are normally distributed, the area under the standard normal curve to the left of ZBAL provides an estimate of the proportion of the population with prewinter energy reserves < EBAL. This area represents the model's estimate of percent mortality due to starvation.

Parameters for estimating ZBAL values are derived from field measurements of endogenous reserves (Table 1). I assume that the animal can catabolize 67% of its fat before death (Torbit et al. 1985b), that each gram of fat yields 9.5 kcal (Kleiber 1975:table 7.3), and that 70% of total calories catabolized are derived from fat and 30% from lean body (Torbit et al. 1985b). For example, I calculate the average energy reserves for does as

$$RES = (FATPER \cdot 0.67 \cdot BW_{in} \cdot 9.5 \cdot 1,000) \div 0.70$$

where

$FATPER$ = proportion of body mass that is fat (g/g),
0.67 = proportion of fat that can be catabolized before death (g/g),
BW_{in} = initial body mass (kg),
9.5 = kcal/g fat catabolized,
$1,000$ = g/kg, and
0.70 = proportion of total calories catabolized from fat.

Model Validation

Study Area.—I tested predictions of the model against field measurements of fatness of the average mule deer doe and fawn and mortality in populations of does and fawns in the Piceance Basin and Middle Park, Colorado. The Piceance Basin in northwestern Colorado is a shrub–woodland dominated by pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*). Deer winter range usually extends from 2,000 m in elevation along Piceance Creek to 2,500 m on the surrounding mesas. In north-central Colorado, Middle Park forms the headwater basin of the Colorado River. Vegetation is predominantly shrub–steppe; big sagebrush (*Artemisia tridentata*) provides a relatively uniform canopy over cool season grasses and forbs. Deer spend the winter between 2,200 and 4,500 m in elevation. Climate in both areas is semiarid. Wallmo et al. (1977) and Bartmann (1983) described these areas in detail.

Input Data.—Weather input was obtained from Green Mountain Dam for simulations of Middle Park deer (National Oceanic and Atmospheric Administration 1967–85) and from the Little Hills Game Research Station for Piceance simulations (National Oceanic and Atmospheric Administration 1972–85). In the strictest sense, the model requires operant temperatures as input. However, because real-time data on daily operant temperatures for the average mule deer are virtually impossible to obtain, approximations are needed. To approximate operant temperatures during validation runs and model experiments, I used hourly estimates of ambient temperatures derived from daily maximum and minimum temperatures following the algorithm of Parton and Logan (1981). I justify this simplification because the model must provide reasonable predictions with readily accessible data if it is to be broadly useful.

Initial conditions for validation runs were set as described (Table 1) for does and fawns in the Piceance Basin. With a single exception, model parameters were derived from values reported in the literature and were not tuned in response to model output. Tuning was required to estimate fat reserves for Middle Park deer because no data were available to set initial conditions for that area. The model consistently overestimated mortality of does and fawns in Middle Park when initial

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conditions for body composition were based on data for Piceance Basin deer. Several ecologists with experience in both areas believed that frequent doe harvest and higher quality range in Middle Park has produced larger, fatter deer relative to those in the Piceance Basin (R. M. Bartmann, L. H. Carpenter, D. J. Freddy, Colo. Div. of Wildl.; G. C. White, Colo. State Univ., pers. commun.). Therefore, I increased initial body weight and fatness of simulated Middle Park does and fawns relative to the body weight and fatness of animals from Piceance (Table 1).

Validation Data.—I compared model predictions to field estimates of total mortality based on ground surveys (R. B. Gill and D. J. Freddy, Colo. Div. Wildl., unpubl. data; Gill 1971; Bartmann 1984; Bartmann and Bowden 1984; Baker and Hobbs 1985) and telemetry studies (White et al. 1987; G. C. White, Colo. State Univ., unpubl. data). I did not use mortality estimates based on band recovery data (White and Bartmann 1983) because winter mortality could not be differentiated from mortality during other seasons. Estimates of dead deer/km^2 from ground surveys were converted to percent mortality of does and fawns using postharvest estimates of the sex and age composition of the population and population size (J. Gray, Colo. Div. Wildl., unpubl. data). Confidence intervals on ground surveys were based on standard errors of dead deer/km^2 and an assumed error of ±15% in estimates of prewinter population size. In cases where estimates of standard errors on numbers of dead deer were not available (e.g., Middle Park, 1971–75), I assumed that the number of dead deer was estimated within ±50% of the mean (Gill 1971:fig. 8). Confidence intervals on mortality rates derived from telemetry data were calculated using binomial standard errors and a normal approximation to the binomial distribution (Simpson et al. 1960: 157).

Although comparing predicted with observed mortality at the end of winter provides a test of the outcomes of the model, it does not validate the mechanisms that produced those results. A more revealing test of the mechanisms represented in the model is provided by comparisons of its output with a time series of measurements throughout the winter. I used observed and predicted daily mortality and body fat levels to achieve this type of validation. I tested the model's cumulative daily predictions of mortality rate during 1982–85 against cumulative daily measurements derived from the telemetry studies of White et al. (1987). Model estimates of percent fat were derived from simulations using weather data for 1 December through 15 April 1982–84 from the Little Hills station, Colorado (National Oceanic and Atmospheric Administration 1982–84) as input. These estimates were compared with field measurements for does (n = 6/month, 1982–83) and fawns (n = 8/month, 1983–84) collected during December, February, and April from the Piceance Basin (Torbit et al. 1988). Initial conditions for percent fat were set using measured values for fatness in October (Torbit et al. 1988). Percentage fat of each animal collected was determined by ether extraction of samples taken from its homogenized carcass (Torbit et al. 1988).

Simulations of overwinter mortality were run from December through March unless >10 cm of snow remained on 31 March, in which case simulations were extended to 31 April. I omitted 1973–74 from the Piceance Basin simulations because 22 days of weather data were missing.

Model Experiments

Meeting model objectives for enhancing understanding of the winter ecology of mule deer depends on performing model experiments. I use experiment here in the sense of planned manipulations of model variables—manipulations used to illuminate the processes being modeled and the relative importance of their component variables.

Sensitivity analysis of models frequently emphasizes changing model parameters by equal amounts and comparing the effect of those changes on model output (e.g.,

Table 2. Characteristics of mild (1976–77) and severe (1978–79) winters in the Piceance Basin, northwestern Colorado. Daily temperatures and snow depths from these winters were used as input in model experiments.

Characteristic	Mild	Severe
Avg max. temp (C)	6.7	2.1
Avg min. temp (C)	−13.2	−14.1
Avg snow depth (cm)	1.4	33.2
No. days with min. temp <−20 C	9	29
No. days with snow depth >10 cm	8	108

Weins and Innis 1974, Steinhorst et al. 1978, Clark and Innis 1982, Hobbs et al. 1982, Fancy 1986, Frederick et al. 1987). This approach implicitly assumes that perturbing model parameters individually or in small groups will provide model outputs that are comparable among perturbations and will thereby reveal which parameters and processes are most influential in determining model behavior. I avoided this approach in model experiments for several reasons. First, different variables offer different ranges of variation. For example, the standing metabolic rate of mule deer is probably estimated within ±5% of the value in the population, whereas measures of body fatness may vary by as much as ±20%. It follows that a 10% increase in these 2 parameters would overestimate the potential importance of standing metabolic rate and underestimate the potential importance of fatness. This problem is exacerbated by the fact that many processes represented in the model are nonlinear and operate in a threshold fashion. Thus, the importance of changing a single variable will depend fundamentally on the value of other variables. This is the case because the outcome of proportional changes in parameters (changes that are inherently linear) will depend on whether those changes occur in the vicinity of thresholds. Consequently, I believe that traditional approaches to sensitivity analysis frequently fail to yield commensurate changes in model predictions.

As an alternative, I chose individual manipulations of initial conditions of variables within ranges that were plausible for those variables and constructed specific experiments to examine interactions. The disadvantage of my approach is that it does not provide direct comparisons of model sensitivity among variables. The advantage is that it does not provide misleading comparisons.

I ran model experiments with parameters (Table 1) set to represent does and fawns in the Piceance Basin using weather data from a severe and a mild winter as input (Table 2). Model manipulations were planned to provide inferences useful in decisions on managing mule deer populations and the habitats they occupy. In particular, I evaluated the efficacy of several prevalent tactics for improving the condition of deer and reducing starvation during winter. These are described in the following sections.

Change Food Quantity and Animal Density.—Managing mule deer to enhance population performance often emphasizes reducing deer population size (reviewed by Short 1979, Connolly 1981) or increasing the standing crops of deer food (reviewed by Wallmo et al. 1981). Each of these tactics is believed to improve the nutritional status of individual animals by making more food available to each deer. To examine the effect of increased food supply and reduced density on starvation, I varied deer density (DENS) from 4 to 60 deer/km² over 5 levels in a factorial arrangement with 5 levels of initial forage biomass (100–1,200 kg/ha).

Improve the Nutritional Quality of Forage.—The chemical composition and physical structure of forages may be more important to the welfare of small ruminants like mule deer than the absolute amount of food available to them (reviewed by Hanley 1982). To examine the role of forage quality in determining mortality in deer, I varied the digestibility of herbs (HRBDIG) from 35 to 45% over 5 levels in a factorial arrangement with 5 levels of shrub digestibility (SHRBDIG = 25–35%). Although the effects of forage cell-wall characteristics on intake are not explicitly represented in the model, these influences were simulated implicitly by changing parameters controlling intake. Under the assumption that dry matter in-

take is influenced by forage physical structure (Spalinger et al. 1986, Baker and Hobbs 1987, Spalinger et al. 1988), I varied total daily intake of dry matter (DMICO = 1.5–2.3% of body mass) together with instantaneous intake rate (CHEWMAX = 1.5–5.5 g/min).

Alter Snow Distribution and Accumulation.—Altering snow distribution and accumulation to increase access to forage and reduce energy costs of travel can be achieved directly by physical intervention (Regelin and Wallmo 1975, Regelin et al. 1977) and indirectly by favoring seral stages of vegetation that maximize snow interception (Hanley 1984, Hanley et al. 1984). The effect of snow on energy costs and energy intake were investigated by varying input data on daily snow depth at 7 levels (−50%, −20%, −10%, 0%, +10%, +20%, +50%). Effects of snow on energy intake were isolated from its effects on expenditure by separately varying snow depth input to model subroutines that calculated energy costs and gains. I also examined the effects of temperature by leaving temperature data from a mild winter unaltered, while changing the snow regime to the severe case. I then compared model output of these simulations with baseline simulations for a mild winter.

Interactions of Animal Density with Quantity, Quality, and Availability of Forage.—Although the above experiments were constructed to isolate the effects of individual perturbations of the model, the management interventions they were designed to mimic realistically cause multiple rather than singular changes in relationships between mule deer populations and their habitats. It follows that interactions among outcomes of management practices may alter their individual, isolated effects. To reveal the importance of interactions of biomass, digestibility, and availability of forage with the density of mule deer populations, I changed the model's formulation representing food supply. In this experiment, food supply was reformulated as a joint distribution of quality and availability following the approach of Sibbald et al. (1979). I also varied the density of deer using that food supply. In so
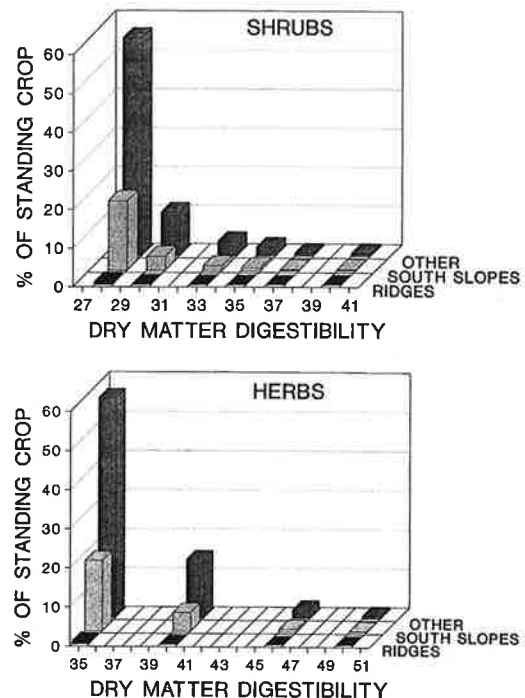

Fig. 2. Hypothetical distribution of digestible energy within forage standing crops on mule deer winter range. I assume that 1% of each energy category occurs on windswept ridges and remains available regardless of snow depth, that 20% occurs on south-facing slopes where snow depth is 20% below the average depth, and that 79% is found in areas where snow depth equals input values.

doing, I assumed (Fig. 2) that forage standing crops were dominated by tissue with low digestibility, but contained small amounts of relatively highly digestible forage (Hobbs and Swift 1985). I also assumed that 1% of the total standing crop occurred on topography where it remained accessible regardless of snowfall (e.g., windswept ridges) and that an additional 20% of forage was found on south-facing slopes where assumed snow accumulation was 20% less than elsewhere. For the purposes of this experiment, I assumed that on each day in the simulation, mule deer consumed the food that yielded the highest energy gain.

Enhance Thermal Cover.—Topography and vegetation that mitigate thermal stress are believed to be important features of habitat for mule deer (Loveless 1967, Black et al. 1975). I tested this belief by varying input for ambient temperatures
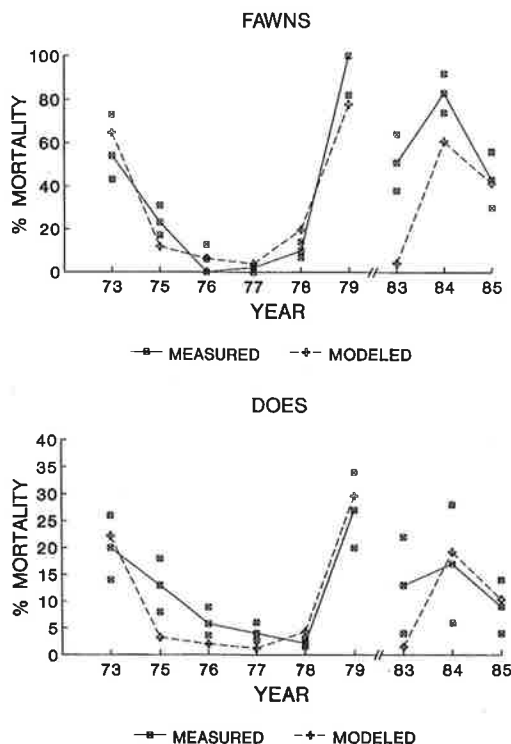
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Fig. 3. Validation of model estimates of mortality in mule deer does and fawns in Piceance Basin in northwestern Colorado. Field measurements of mortality during 1972–79 include deaths from all causes based on Bartmann (1984) and Bartmann and Bowden (1984). Field measurements for does during 1983–85 are means from the Colorado Federal Shale Oil Tract (CB) and Little Hills (LH) study areas (all sources of death included for winter months only; G. C. White, Colo. State Univ., unpubl. data). Field measurements for fawns during 1983–85 are based on starvation losses from the LH study area during winter (White et al. 1987). The CB study area was excluded because of high levels of predation observed there. Upper and lower squares represent 95% confidence limits on field estimates.

by $-50\%, -20\%, -10\%, 0\%, +10\%, +20\%$, and $+50\%$ during mild and severe winters. I also examined the effects of temperature by changing the temperature regime of a mild winter to the severe case while leaving the snow regime of the mild winter unaltered. I then compared model output of these simulations with baseline simulations for a mild winter.

Improve Condition of Animals in Autumn.—It has been argued that habitat improvements aimed at summer and transition habitats, improvements that enhance the energy reserves of animals arriving on winter ranges, may achieve greater benefits than actions directed at winter ranges themselves (Mautz 1978: 342). To evaluate the efficacy of improving prewinter condition on reducing overwinter mortality, I varied fatness over 5 levels (9–13% for does, 2–8% for fawns) in a factorial arrangement with 4 levels of body size (50–70 kg for does, 20–35 kg for fawns). Moreover, although condition of the average animal is frequently believed to offer a sufficient indicator of the relative condition of the prewinter population, individual variation in condition may be equally important in determining rate of starvation. To investigate this interaction, I varied fat reserves over 5 levels (*see* above) in a factorial arrangement with the coefficient of variation for fatness (15%, 20%, 25%).

Reduce Disturbance.—Although it is clear that disturbance by people can increase the energy costs of mule deer, the significance of that increase for animal survival remains poorly understood (Freddy et al. 1986). I compared 3 regimes of disturbance with the undisturbed state. I assumed disturbance occurred 1, 7, or 14 times weekly and that each disturbance caused the average deer to travel 50, 100, 250, or 500 m that it would not have moved in the absence of disturbance. I assumed that deer fled through untracked snow (RMUL = 1.0) at a speed of 100 m/minute.

Provide Supplemental Feed.—Development of concentrate rations that can be fed to starving mule deer without causing digestive disorders has provided an efficacious, if expensive, management alternative for reducing mortality of mule deer during winter (Baker and Hobbs 1985). To simulate alternative feeding regimes, I increased metabolizable energy intake by 100–1,000 kcal/day over 10 levels in a factorial arrangement with starting date for supplementation (1 Jan, 1 Feb, 1 Mar).

RESULTS

Model Validation

Trends in model predictions of mortality in mule deer resembled trends in mea-
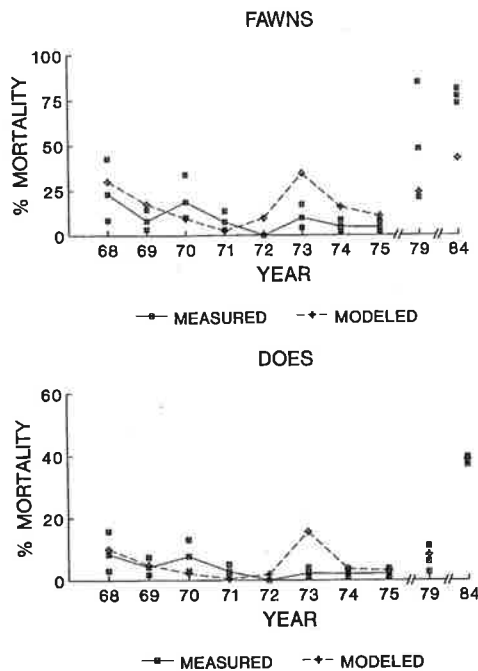
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Fig. 4. Validation of model estimates of mortality in mule deer does and fawns in Middle Park in west-central Colorado. Field data include all causes of mortality (R. B. Gill and D. J. Freddy, Colo. Div. Wildl., unpubl. data; Gill 1971; Baker and Hobbs 1985). Upper and lower squares represent 95% confidence limits on field estimates.
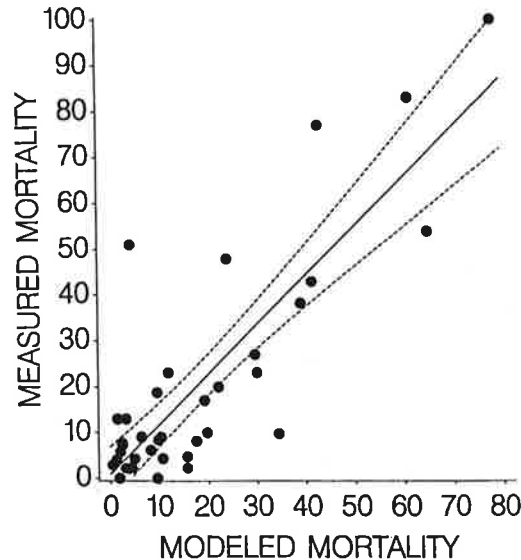

Fig. 5. Measured values for mortality for does and fawns from all study areas and years regressed against model predictions of mortality. Equation is given by $Y = 0.88 + 1.08X$ ($r^2 = 0.71$, $P = 0.0001$). Dashed lines show 95% confidence intervals on the mean prediction of measured mortality.

sured values during most years. Simulated mortality fell within 95% confidence limits on measured values of doe mortality during 13 of 19 years and agreed with measured fawn mortality during 9 of 19 years (Figs. 3, 4). Overall, model predictions accounted for 71% of the variation in measurements of mortality (Fig. 5). The slope of the regression of model predictions vs. measured values did not differ from 1 ($P = 0.67$) and the intercept did not differ from zero ($P = 0.30$), indicating there was no consistent tendency for the model to over- or underestimate measured mortality. However, examination of the time series data (Figs. 3, 4) showed that the model frequently underestimated fawn mortality during years immediately following severe winters. Temporal patterns in predictions of daily mortality resembled observed patterns except during 1982–83 (Fig. 6).

Model estimates of the percentage of body fat in does and fawns closely tracked measured values during early and midwinter, but exceeded measured values at winter's end (Fig. 7). Model predictions accounted for 72% of the variation in measured fat levels (Fig. 8). The slope of the regression of model predictions vs. measured values did not differ from unity ($P = 0.54$), nor did the intercept differ from zero ($P = 0.25$).

Simulations of Energy Budgets

Model predictions of total energy expenditure during a mild winter exceeded predicted expenditure during a severe one, despite increases in costs of thermoregulation and activity in response to severe weather (Table 3). This seeming paradox occurred because energy intake was greater during a mild winter, and, hence, weight loss was substantially less. Thus, because deer were heavier and because energy expenditure is strongly influenced by body mass, total energy costs were greater during mild winters than severe ones. Mass specific energy costs reflected the effect of winter weather on energy expenditure

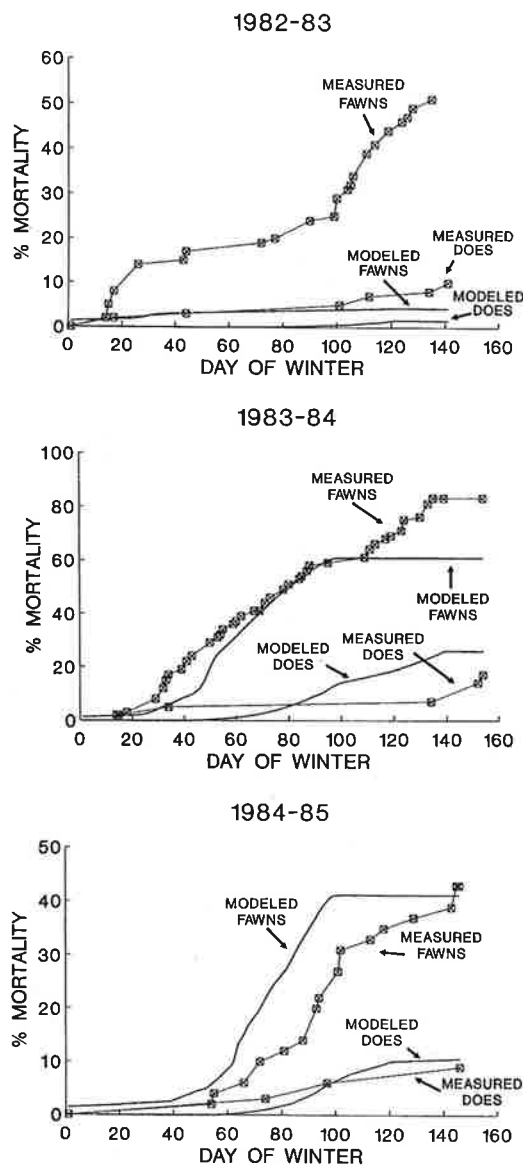### 1982-83

1983-84

1984-85

Fig. 6.   Validation of model predictions of cumulative mortality in mule deer does and fawns in the Piceance Basin in northwestern Colorado during 1982–85. Field estimates of daily mortality from G. C. White, Colo. State Univ., unpubl. data.
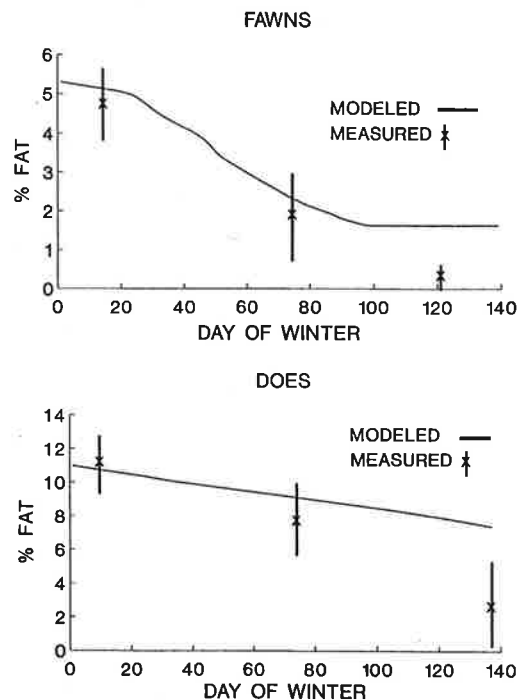
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Fig. 7.   Validation of model predictions of percent body fat in the average mule deer doe and fawn from the Piceance Basin in northwestern Colorado. Field data taken from Torbit et al. (1988).

would appear to have greater intakes than heavier ones.

Predictions of weight-specific energy costs of thermoregulation increased by more than 10 times in does and increased 45 fold in fawns during a severe winter
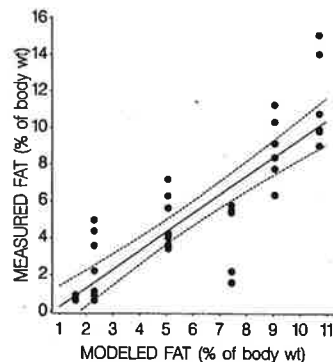

Fig. 8.   Measured values for fatness of does and fawns regressed against model predictions of fatness. Equation is given by $Y = -0.75 + 1.01X$ ($r^2 = 0.72$, $P = 0.0001$). Dashed lines show 95% confidence intervals on the mean prediction of measured fatness.

more clearly than total costs did. However, because total daily intake was a function of initial body weight rather than current body weight, expressing energy intake on the basis of metabolic body size (which changes as the animal loses weight) would be misleading because lighter animals

Table 3. Simulated energy budget for mule deer does and fawns during mild and severe winters,[a] Piceance Basin, Colorado.

	Energy costs (Kcal)		Energy costs (Kcal/kg$^{0.75}$)		% of total	
	Severe	Mild	Severe	Mild	Severe	Mild
Does						
Resting						
Lying	121,336	132,017	6,521	6,575	65.1	68.4
Thermoregulation	4,366	329	222	16	2.3	0.2
Ruminating	1,018	1,098	55	55	0.5	0.6
Activity						
Posture	41,516	43,350	2,230	2,159	22.3	22.5
Net locomotion	2,076	2,149	112	107	1.1	1.1
Net locomotion (snow)[b]	1,708	27	91	1	0.9	0.0
Thermoregulation	1,021	52	30	1	0.5	0.0
Eating	9,314	9,963	499	496	5.0	5.2
Other						
Gestation	4,074	4,074	238	212	2.2	2.1
Total	186,549	193,037	10,019	9,621		
Fawns						
Resting						
Lying	83,059	92,230	8,324	8,368	76.5	78.7
Thermoregulation	1,669	49	161	4	1.5	0.0
Ruminating	648	716	65	65	0.6	0.6
Activity						
Posture	18,789	20,092	1,882	1,823	17.3	17.1
Net locomotion	852	901	85	82	0.8	0.8
Net locomotion (snow)[b]	213	7	53	1	0.5	0.0
Thermoregulation	213	0.0	20	0.0	0.2	2.7
Eating	2,880	3,181	288	289	2.7	2.7
Other						
Gestation	0.0	0.0	0.0	0.0	0.0	0.0
Total	108,641	117,176	10,879	10,632		

[a] Input data for severe winter taken from daily weather records for 1978–79 and from records for 1976–77 for mild winter (Table 2).
[b] Net cost of traveling in snow above locomotion cost on bare ground.

(1978–79) relative to a mild one (1976–77) (Table 3). During a severe winter, ambient temperatures exceeded the resting lower critical temperature of mule deer during almost 9 of every 10 hours (T > LCT$_l$, 89% of the time for does, 87% for fawns). Because thermoregulation costs remained a relatively small proportion of the animal's overall energy budget, energy expended to meet thermoregulation costs during a severe winter increased total weight specific costs by only 4% in does and 2% in fawns relative to their expenditures during a mild winter. However, although thermoregulation costs remained a small part of the animal's total expenditure during a severe winter, offsetting these costs would nevertheless require catabolizing a substantial fraction of the animal's energy reserves (9% in does, 15% in fawns) if those costs could not be offset by dietary energy.

Effects of a severe winter on activity costs also were relatively minor (Table 3). Energy costs of walking in snow contributed a small portion of the animal's total energy budget, even when snows were deep. Energy expenditure for travel in snow was unimportant because of the slow travel speeds of simulated mule deer during foraging (1.5 m/min). At these speeds, the influence of snow on travel costs is small (Parker et al. 1984). Consequently, the single model parameter that required a "guess" for initial conditions (RMUL) exerted a largely trivial influence on model behavior.

Severe winter weather had greater im-

Table 4. Simulated intake of dry matter and metabolizable energy (ME) of mule deer does and fawns during a mild and severe winter,[a] Piceance Basin, Colorado.

Source	Dry matter (kg)		ME (Kcal)		% of total ME	
	Severe	Mild	Severe	Mild	Severe	Mild
Does						
Herbs	16.4	98.1	22,659	135,089	17.0	83.8
Shrubs	107.0	25.4	110,521	26,199	83.0	16.2
Total	123.4	123.4	133,183	161,293		
Fawns						
Herbs	11.7	76.0	16,105	96,022	17.0	83.8
Shrubs	76.0	18.0	78,556	18,623	83.0	16.2
Total	87.7	87.7	94,663	114,644		

[a] Input data for severe winter taken from daily weather records for 1978–79 and from records for 1976–77 for mild winter.

pact on energy intake than energy expenditure. Although weather during a severe winter did not change the total amount of dry matter consumed by mule deer relative to their consumption during a mild winter, it markedly reduced total energy intake (Table 4). These reductions resulted from an increased proportion of shrubs in the diet and consequent reductions in diet digestibility.

Severe winter weather can accelerate catabolism of reserves by retarding the animal's rate of energy intake and by accelerating its rate of expenditure. Seventy-five percent of the difference in energy balance between a mild and a severe winter was attributable to reductions in energy intake (Fig. 9). Thus, simulated energy balance and starvation mortality in mule deer during winter were strongly controlled by the number of days that snow conditions forced animals to consume diets containing low levels of available energy.

Model Experiments

Change Food Quantity and Animal Density.—Changing input weather data from a mild to a severe winter caused a greater change in mortality in does and fawns than was caused by a 10-fold change in the amount of food available to each deer at the beginning of winter (Fig. 10). Increasing food supplies above 200 kg/ha exerted negligible effects on simulated mortality during mild and severe winters. Changing deer density did not change the relationship between food supply and mortality; model predictions were relatively insensitive to deer density except when prewinter food supplies were reduced to 75 kg/ha and deer densities were increased to 60 animals/km². However, under these conditions, the entire standing crop of herbs was consumed and mortality accelerated rapidly. When biomass exceeded 400 kg/ha, >75% of the standing crop of shrubs and 50% of the herbs remained uneaten at the end of winter, even in the face of exceptionally high densities of deer (Fig. 11).

Mortality was relatively insensitive to initial food supply and deer density because the only mechanism relating these
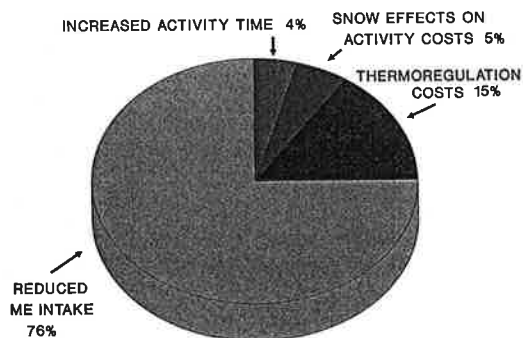

Fig. 9. Influences of winter weather on simulated energy balance of the average mule deer doe. Percentages give the proportion of the difference in energy balance between mild and severe winters that was attributable to effects of weather on energy expenditure and intake. Increased activity time represents the elevation in energy expenditure required by spending more time feeding; snow effects on activity reflect the elevation in energy expenditure required to travel through snow independent of increases in activity time.
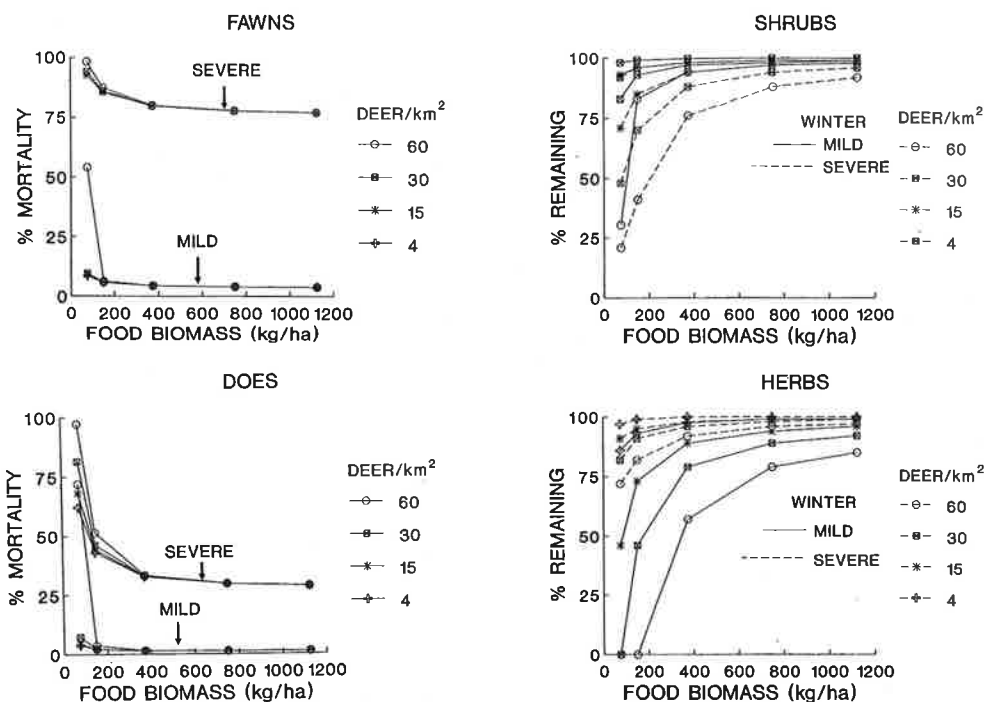
Fig. 10. Simulated mortality resulting from starvation of mule deer does and fawns relative to initial conditions for total food biomass and deer density during mild and severe winters. I assume that food supply is composed of one-third herbs and two-thirds shrubs at all biomass levels.

Fig. 11. Simulated proportion of the initial standing crop of shrubs and herbs remaining at the end of mild and severe winters relative to initial conditions for forage biomass and deer density. I assume that forage biomass is composed of one-third herbs and two-thirds shrubs at all biomass levels.

parameters to energy balance was the influence of food biomass on eating rate. Because this relationship is asymptotic, increases in the amount of food available to each deer caused by increasing initial food supply or reducing deer densities failed to influence energy balance unless initial food supplies fell below the asymptote in the representation of dry matter intake rate as a function of quantity.

Improve the Nutritional Quality of Forage.—Model predictions were highly sensitive to changes in initial conditions influencing energy gain, and these influences showed strong interactions. During a severe winter, the effect of digestibility of herbs was negligible, but each percentage point increase in the digestibility of shrubs in the average doe's diet resulted in about 10% points less mortality (Fig. 12). During mild winters, the influence of the digestibility of shrubs depended strongly on the digestibility of herbs (Fig. 12). In-

creasing digestibility of herbs above 40% had almost no impact on mortality during a mild winter regardless of shrub digestibility. Although mortality levels for fawns were consistently higher than those seen in does, the effects of changes in digestibility were otherwise similar.

Changing daily dry matter intake (DMICO) caused fundamental shifts in model predictions (Fig. 13). The magnitude of these changes depended on the value of maximum instantaneous intake (CHEWMAX). When CHEWMAX exceeded about 2.5 g/minute, the model was more sensitive to the limit on total daily intake (DMICO) than to CHEWMAX; below that point, CHEWMAX was the more sensitive variable. Thus, the interaction between DMICO and CHEWMAX was strongest in the vicinity of values of 2.5 g/minute for CHEWMAX. This was the case because when CHEWMAX declined below 2.5 g/minute, it became increasing-
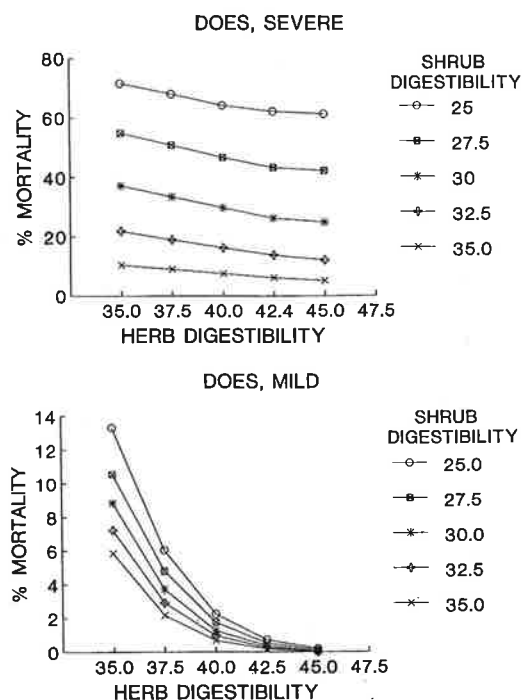
Fig. 12. Simulated mortality due to starvation of mule deer does during a severe and a mild winter relative to initial conditions for dry matter digestibility of herbs and shrubs.

Fig. 14. Simulated overwinter activity time, energy expenditure for activity, and energy intake of the average mule deer doe relative to maximum instantaneous intake during a severe winter. Curves based on daily intake rate of 1.7% of body mass/day.

ly difficult for simulated deer to make an energetic profit by feeding (Fig. 14). At 2.5 g/minute maximum intake, energy costs of feeding exceeded the energy gains obtainable from feeding about 1% of the time, but when CHEWMAX was 1.5 g/minute, deer failed to profit from feeding about 30% of the time. Whenever the costs of feeding exceeded the energy gained
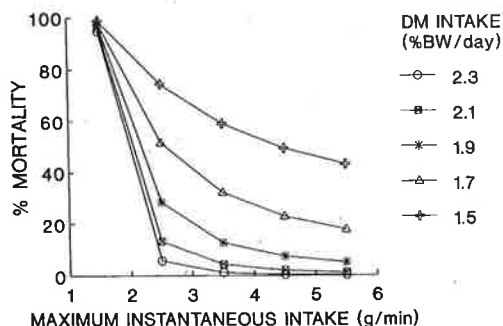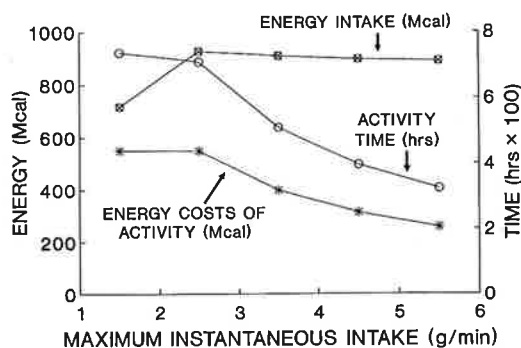

Fig. 13. Simulated mortality due to starvation of mule deer does relative to initial conditions for daily dry matter intake (% of body mass/day) and maximum instantaneous intake (g/min).

from feeding, dry matter intake was reduced to zero and energy intake dropped sharply. However, whenever feeding was profitable, decreasing values of CHEWMAX increased time spent feeding and, hence, energy expenditure.

Achieved levels of daily dry matter intake were not constrained by the time available for feeding until the maximum daily intake (DMICO) exceeded 2.5% of body weight or until CHEWMAX fell to 0.75 g/minute. Thus, whenever daily intake was > 2.5% of body weight or CHEWMAX was < 0.75 g/minute, the animal could not compensate for a reduced rate of feeding by increasing feeding time.

Alter Snow Distribution and Accumulation.—Proportional changes in snow depth caused virtually no change in mortality of does or fawns during a mild winter (Fig. 15). This was the case because during much of the winter, there was no snow cover and, consequently, percentage changes in snow depth remained equal to zero. However, changing the snow regime for a mild winter to the severe case without altering temperatures caused major increments in mortality relative to the baseline output for a mild winter (72.1% vs. 4.2% in fawns, 22.7% vs. 1.3% in does). Reducing snow accumulation during a severe winter by 30% reduced mortality by almost 50% in does and fawns. Most of this reduction was caused by increasing the availability of forage rather than by re-

FAWNS

SEVERE

EFFECT OF SNOW ON
-○- ACTIVITY ALONE
-■- FOOD ALONE
-✱- ACTIVITY & FOOD

MILD

DOES

SEVERE

EFFECT OF SNOW ON
-○- ACTIVITY ALONE
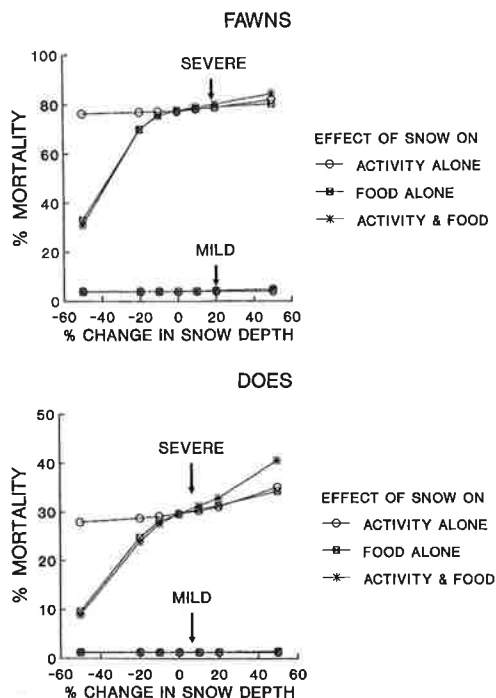-■- FOOD ALONE
-✱- ACTIVITY & FOOD

MILD

Fig. 15. Simulated mortality due to starvation of mule deer does and fawns relative to changes in daily snow depth during a mild and a severe winter. Curves represent separate and combined effects of snow on availability of forage and energy costs of activity. Curve for effects of snow on energy expenditure assumes no influence of snow on energy intake; curve for effects on food alone assumes no effect of snow on energy expenditure.

FAWNS

DEER/km^2
-○- 60
-■- 30
-✱- 15
-◆- 4

DOES
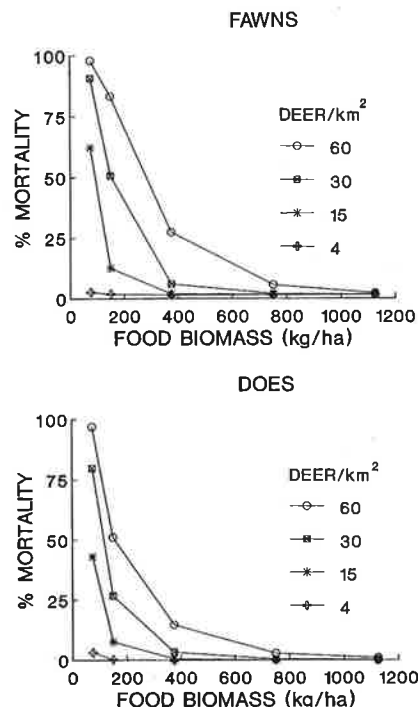

DEER/km^2
-○- 60
-■- 30
-✱- 15
-◆- 4

Fig. 16. Simulated mortality due to starvation of mule deer does and fawns during a severe winter relative to initial conditions for forage biomass and deer density. Forage biomass is modeled as a density function of dry matter digestibility and forage availability (Fig. 1). I assume the total food biomass is composed of one-third herbs and two-thirds shrubs.

ducing energy costs of activity. Simulated increases in snow depths above baseline values for a severe winter failed to substantially increase mortality. This was the case because snow depths in model experiments never exceed the height of the shrub layer. If this had occurred, mortality would have rapidly increased to 100% in both does and fawns.

Interactions of Animal Density with Quantity, Quality, and Availability of Forage.—Animal density and food biomass exerted strong control on mortality (Fig. 16) when the digestibility and availability of food was variable (Fig. 2). When food biomass fell below 400 kg/ha, differences in mortality due to differences in density within a severe winter (Fig. 16) nearly equaled the differences in mortality between a mild and severe winter at the same density (Fig. 10). The greatest effects

of density were seen at low biomass, and the greatest effects of biomass were seen at high density. Given sufficiently low density (3.75 deer/km²), winter mortality was virtually eliminated in both does and fawns even during a severe winter. The increased sensitivity of model predictions to changes in deer density and food amount resulted from coupling these parameters to the digestibility of deer diets, a link that was achieved when food supplies were represented as a distribution of varying quality, but was not present when food supplies were represented without variation in their nutritional value.

Enhance Thermal Cover.—Increasing ambient temperatures above baseline values had negligible effects on mortality of does and fawns during mild and severe winters (Fig. 17). However, reducing temperatures below those in baseline runs increased mortality during a severe winter,
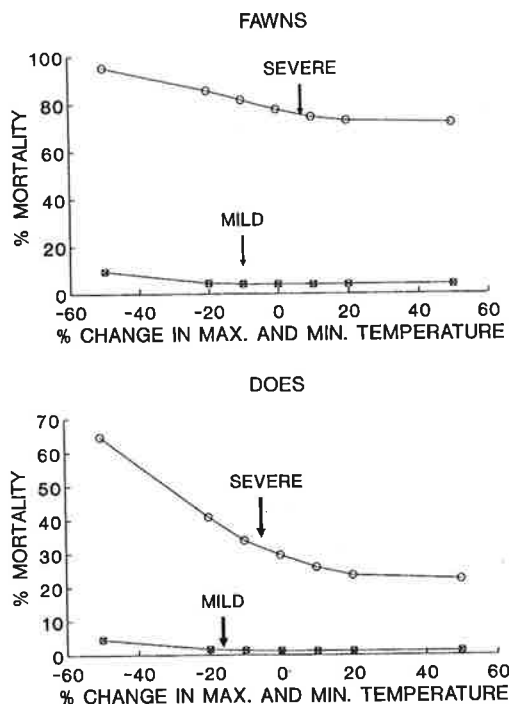
Fig. 17. Simulated mortality due to starvation in mule deer does and fawns during mild and severe winters relative to changes in maximum and minimum daily temperatures.
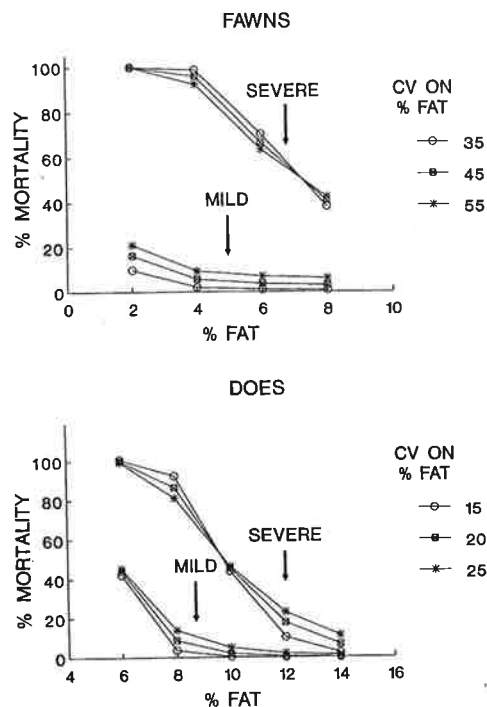
Fig. 18. Simulated mortality due to starvation in mule deer does and fawns during mild and severe winters relative to initial conditions for average percent body fat and its coefficient of variation.

particularly in does. The steep increase in doe mortality is attributable to the relatively low variance in their fat reserves (CV = 21%), which caused the shape of their fat reserve distribution to be narrow. As a result of this shape, small changes in values for overwinter energy balance in the vicinity of the rising portion of the fat reserve curve caused rapid increases in mortality. This was less true for fawns who had a high variance in fat reserves (CV = 45%), and hence, a flatter, broader, distribution. It should be remembered, however, that the baseline temperatures in these simulations (0% change) were taken from an exceptionally severe winter. The extreme temperature regime (−50% change) is probably only encountered at the northern limits of mule deer range.

Changing input data for a mild winter to reflect severe temperatures with mild snow depths caused small increases in mortality relative to the baseline simulations for a mild winter (2.3% vs. 1.3% in does,

5.7% vs. 4.2% in fawns). This was the case because even during mild winters, temperatures are not markedly different from those encountered during severe ones (Table 2) and because energy costs of thermoregulation were a relatively small portion of the animal's total energy expenditure (Table 3).

Improve Condition of Animals in Autumn.—Predictions of starvation mortality were extremely sensitive to changes in the fatness of does and fawns at the beginning of winter (Fig. 18). Within the range of 8–12% body fat in does and 4–8% in fawns, a single percentage point change in fatness at the beginning of a severe winter shifted mortality by about 15% points at its end. Outside that range, the effect of fatness was less dramatic. During a mild winter, mortality was low and largely uninfluenced by fatness until the percentage of body fat fell below about 9% in does and below about 4% in fawns.
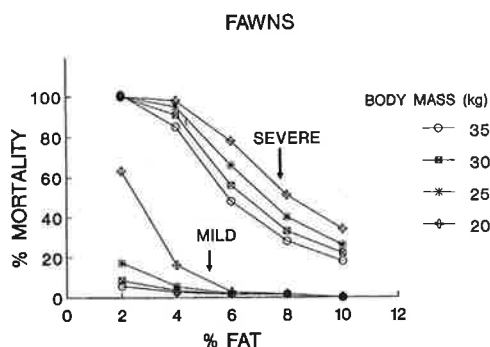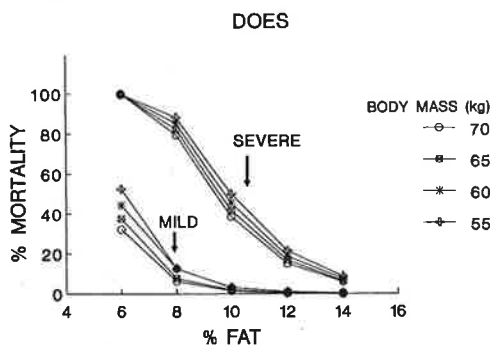
FAWNS

BODY MASS (kg)
- 35
- 30
- 25
- 20

DOES

BODY MASS (kg)
- 70
- 65
- 60
- 55

Fig. 19. Simulated mortality due to starvation in mule deer does and fawns during mild and severe winters relative to initial conditions for average % body fat and body mass.

FAWNS

DISTURBANCES PER WEEK
- 1
- 7
- 14

DOES

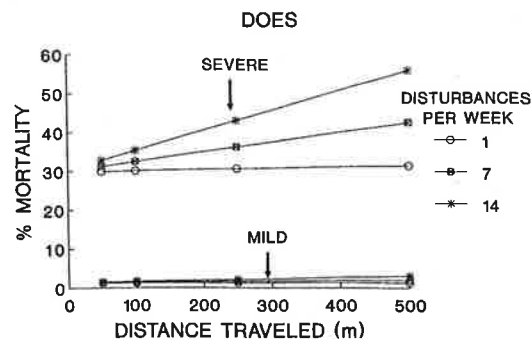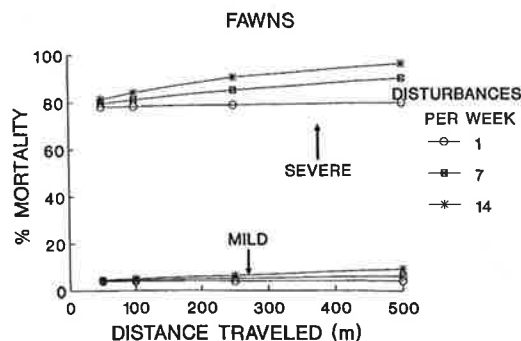DISTURBANCES PER WEEK
- 1
- 7
- 14

Fig. 20. Simulated mortality due to starvation in mule deer does and fawns during mild and severe winters relative to frequency of disturbance and distance traveled per disturbing event.

CV ON % FAT
- 35
- 45
- 55

CV ON % FAT
- 15
- 20
- 25

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The effect of average fatness on population mortality depended on the variation in fat reserves in the population. Changing coefficients of variation in percent fat from 35% to 55% in fawns caused an almost 3-fold increase in mortality in fawns during a mild winter. The intersection of curves representing different coefficients of variation for fat occurs at exactly 50% mortality in the population (Fig. 18). This point, in turn, corresponded to the level of fatness that provided calories equal to those needed to offset energy deficits in the average animal. To survive a severe winter, the average fawn required less prewinter body fat (ca 7.5%) than the average doe (ca 10%) by virtue of its higher dry matter intake rate (2.9% of body weight for fawns, 1.7% for does). However, simulated mortality was consistently higher for fawns because their realized fat levels (5% of body mass) were well below their average requirement, whereas fat levels in simulated does (11% of body mass) exceeded it.

The effect of fat reserves depended on body size, particularly in fawns (Fig. 19). This dependence resulted from the effects of body size on total calories in fat, as well as its effects on energy intake and expenditure. Decreasing body size tended to elevate mortality rates at given fat level, but this tendency was greatest at intermediate values for body fat. Mortality rate was less sensitive to effects of body weight at high and low fat levels.

Reduce Disturbance.—Daily disturbance markedly increased simulated mortality in does and fawns during a severe winter (Fig. 20). The extreme case (2 disturbances/day, each causing animals to move 500 m) almost doubled mortality of does. Mortality was insensitive to disturbance during a mild winter.

Provide Supplemental Feed.—Predictions of mortality in does and fawns responded sharply to simulated supplemental feeding during a severe winter (Fig. 21). If feeding was begun by 1 February,
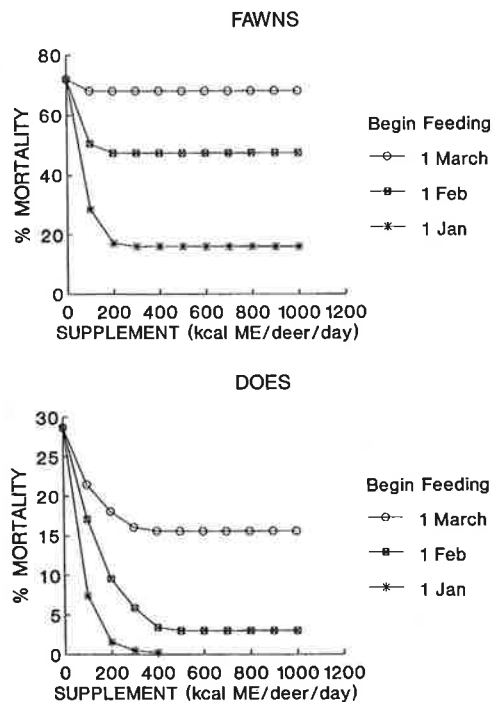
FAWNS

DOES

Fig. 21. Simulated mortality due to starvation in mule deer does and fawns during a severe winter relative to level of supplemental feeding and its initiation date.

mortality could be virtually eliminated in adult does and reduced to <20% in fawns by feeding rations providing 200 kcal/$kg^{0.75}$/day. However, if initiating feeding was delayed beyond early February, it rapidly became impossible to avert significant mortality regardless of feeding level. These simulations implicitly assumed that animals have reasonable access to shrubs (Table 1). When shrubs become less available as a result of a lower shrub canopy, lower initial biomass, or deeper snow than was the case in these simulations, more supplement will have to be fed at earlier dates to reduce mortality significantly.

DISCUSSION

Simulation models have become widely accepted as useful adjuncts to traditional analysis tools in wildlife management (see reviews of Connolly 1978, Grant 1986, Starfield and Bleloch 1986, Walters 1986). To be most useful in this role, a simulation model must be predictive, revealing, and accessible. A model should provide a reasonable level of predictive power, thereby reducing uncertainty about the biological consequences of decisions. Simple regression equations can predict mortality in mule deer based on environmental input at a high level of precision and can achieve those predictions with far less complexity than is required by a simulation approach (Bartmann and Bowden 1984). However, a successful simulation model represents plausible mechanisms causing mortality and, in so doing, reveals inferences that would not otherwise emerge from the individual studies upon which the model is based or from purely predictive, regression approaches. These inferences, in turn, touch on many decisions in habitat and population management.

To influence those decisions, however, a successful model must be accessible—it must be constructed to allow its use by persons unfamiliar with computer simulations, as well as those accustomed to them, and should be driven by input data that can be obtained with a reasonable investment. There is a fundamental conflict between realism and utility in simulation models; increased biological realism usually must be bought with more detailed input, obtainable only at increased expense. Thus, keeping in mind that models are first of all abstractions, the most useful models will achieve a careful compromise between the realism of the natural world and the input data needed to represent it. There are several published models that simulate energy balance in cervids (Swift 1983, Boertje 1985, Hudson and White 1985a, Fancy 1986). Their utility in influencing management decisions has been limited, however, by an absence of formal validation (but see Fancy 1986), by formidable input requirements (e.g., Swift 1983), and by implementations that require the author's participation or a relatively high level of programming skill by the user to manipulate the model.

Model Validation

Agreement of the predictions of my model with results of field surveys does not

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permit the conclusion that the model can accurately predict mortality in mule deer populations. Field measurements have their own biases. Helicopter census of pre-winter population size probably underestimates the denominator in mortality estimates on shrub–woodland ranges (Bartmann et al. 1986), and removal of carcasses by predators may bias estimates of the numerator (Bartmann 1984). Telemetry studies of mortality are less subject to bias (although the effect of stress of capture and handling is not well understood), and it is encouraging that model predictions mimicked results of these studies as well as field surveys during most years. However, despite sources of error in data and occasional lack-of-fit in model predictions to those data, the resemblance of the estimates of the model to field measurements allows reasonable confidence in the ability of the model to represent processes of starvation in mule deer and to offer predictions that approximate what can be obtained by widely used, empirical approaches.

The agreement of model predictions with field data on mortality in mule deer does from 2 different winter ranges emphasizes the importance of starvation as cause of death, at least in adult females. If other sources are strongly operative, sources not represented in the model, they appear to be compensatory with starvation; otherwise, the model's predictions of starvation mortality would not track field estimates of total mortality as closely as they did.

The agreement of model predictions with empirical data, although reasonably close, was not perfect. These imperfections are revealing. The poorest fit between observed and predicted values occurred during 1982–83 in the Piceance Basin. Diarrhea was observed in many of the fawns collared in the telemetry studies of mortality during that year (L. H. Carpenter, Colo. Div. Wildl., pers. commun.). As a result, animals may have died of disease rather than starvation. This illustrates that although starvation and its compensatory sources of mortality may be the usual cause of death on these winter ranges, other

sources may periodically predominate and may be additive to starvation losses.

The model frequently underestimated mortality rates in fawns and overestimated condition of does and fawns at the end of winter. Observed daily mortality frequently showed a surge of deaths in fawns at the end of winter that was not tracked by model predictions (Fig. 6). These discrepancies suggest that processes that are influential in nature are not represented in the model. Carry-over effects of severe weather on animal condition between years may be one such process. Measured mortality rates frequently exceeded model predictions of mortality during the years immediately following severe winters. This suggests that the loss of condition incurred by deer during extreme weather may persist into subsequent years, even when those later years are relatively mild.

Several processes influencing energy intake were not represented in the model and probably should be included in later versions. Snow conditions on winter ranges are exceedingly dynamic during late winter and early spring; crusting and changes in snow density and moisture content contribute to these dynamics, which, in turn, may profoundly affect the availability of forage and the energy costs of activity (Parker et al. 1984; Fancy and White 1985b,c). Although daily snow density can be input to the model, validation runs assumed a constant density in the absence of such data. Thus, because these changes in snow characteristics may magnify energy deficits, they also may explain the divergence between model predictions and field measurements during late winter, particularly the model's failure to mimic a late season acceleration in fawn mortality. Moreover, validation runs were set up such that forage quality remained constant throughout winter. If deer consumed the most nutritious foods early in the season, observed mortality could increase dramatically when the supply of those foods was exhausted. Seasonal changes in intake rates of adults (Wood et al. 1962, Nordan et al. 1968, McEwan 1975, Bahnak et al. 1981) offer another potentially influential process not incorporated in the model. Ob-

served fat reserves in Piceance does may have been lower than predicted ones during a mild winter (Fig. 7) as a result of seasonality in metabolism that caused weight losses independent of those predicted by the model.

Model Experiments

A pivotal revelation of the modeling effort was that processes controlling energy intake were generally more influential in determining starvation mortality than were processes controlling energy expenditure. A similar outcome has been seen in other simulation studies (Swift et al. 1980, Wickstrom et al. 1984, Fancy 1986). However, it can be argued that model predictions of energy expended for thermoregulation underestimate the true expenditure because simulations used ambient temperatures rather than operant temperatures as input and thus failed to specifically represent conductive, convective, and radiative heat losses (Moen 1968a,b,c). The model's algorithm for estimating thermoregulation costs is, indeed, simplified, but it is uncertain whether this simplification caused under- or overestimation of true energy costs.

To the extent that model predictions exceeded the true costs, we can have greater confidence in the conclusion that the real costs are not dominant components of the energy budget. Major overestimation of thermoregulation costs could result from the model's failure to represent heat gains from solar radiation during the day. Mule deer that were shivering before sunrise stopped shivering thereafter, with no change in measured ambient temperature (Parker and Robbins 1984). Other sources of overestimation include the animal's selection of favorable microclimates to mitigate heat loss. Although these sources of energy gain may fail to compensate for unrepresented sources of energy losses (conduction, convection, radiation), I believe the model's fundamental conclusions on the importance of thermoregulation remain robust. Major elevations in temperature regimes for mild and severe winters failed to substantially perturb model pre-

dictions of mortality. Regression studies also revealed that winter temperatures have a minor impact on mortality in mule deer (Bartmann and Bowden 1984).

In practical terms, it appears that enhancing thermal cover on shrub–steppe and shrub–woodland winter ranges will be ineffectual in improving condition of mule deer. This prediction has been corroborated empirically (D. J. Freddy, Colo. Div. Wildl., unpubl. data). However, I observed important thresholds in the relationship between simulated mortality and temperature, particularly for does (Fig. 15). These suggest that cover may be substantially more important at more northerly latitudes. Moreover, these thresholds imply that loss of existing cover (as opposed to cover enhancement) could markedly alter patterns of mortality.

Given the sensitivity of model predictions to variation in energy intake, it is important to identify variables that influence this process. Changing initial conditions for 3 variables (maximum daily intake of dry matter, maximum instantaneous intake of dry matter, and dry matter digestibility) caused qualitative changes in model behavior. All of these variables, in turn, respond to physical characteristics of forages, particularly the thickness of forage cell wall and its lignification (Spalinger et al. 1986, 1988; Baker and Hobbs 1987). These physical characteristics are relatively homogeneous within major forage groups (mature and senescent forbs, grasses, and leaves and stems of shrubs). This suggests that physical characteristics of diets that result from particular mixtures of forages should be used to drive energy intake. However, representing the physiological influence of forage physical structure on energy intake (even at the relatively crude level at which we currently understand that influence) depends first on understanding feeding behavior. We cannot predict the consequences of diet choices until we can predict the choices themselves, and, at the moment, the former is better understood than the latter.

Until this is achieved, I surmise that because variables controlling energy intake would move in the direction of reducing

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mortality and enhancing animal condition whenever diets contain low levels of cell wall, managers should emphasize habitat improvement prescriptions that offer palatable forages with low cell-wall content to wintering mule deer. These include immature grasses and leaves of shrubs and forbs. It should be emphasized that these need to be present only in relatively small amounts (Figs. 2, 16) to have a substantial impact on winter mortality. If snow accumulation renders such forage unavailable, then habitat managers should look to transition ranges to improve fat reserves of animals before winter begins.

Body fat content emerged as a highly influential variable in the model (Figs. 18, 19). This emphasizes that application of the model will depend on obtaining reasonable estimates of fat levels in the population of interest. Fortunately, recently developed regressions between kidney fat and whole body fat make such determinations feasible on a relatively large scale (Torbit et al. 1988).

The influence of fat reserves on mortality depended on body size, particularly in fawns (Fig. 19). Small increases in body fat caused large increases in survival of small fawns, but increasing body size of lean fawns conveyed relatively small advantages. The survival value of increasing body size in simulated deer with high fat levels resulted from the scaling of intake rate and energy expenditure relative to body size. Increasing body size elevated energy intake (which scaled to $BW^{1.0}$) more rapidly than energy requirements (which scaled to $BW^{0.75}$). Although increased body mass clearly conveys a survival advantage at a given level of body fat, the interaction of size and fatness illustrates why body size is an imprecise predictor of survival in mule deer fawns (White et al. 1987:fig. 2). The spread of points in Figure 19 illustrates that body size will be poorly related to survival if fat levels vary among animals of different size within age classes. Body size is apparently not well correlated with fatness within age classes of mule deer (Torbit et al. 1988:fig. 1).

Increasing food amount and reducing animal numbers are the predominant tools

of mule deer management in the West. At first look, the model seems to suggest that these frequently used approaches will be ineffectual at reducing mortality (Fig. 10). Empirical evidence offers limited support for this suggestion. Bartmann and Bowden (1984) failed to find any relationship between prewinter population density of mule deer and the rate of overwinter mortality in those populations (but also *see* Gilbert et al. 1970:22). Moreover, during a severe winter, Baker and Hobbs (1985) observed exceedingly high levels of mortality in mule deer using sagebrush range that had been extensively treated to improve its value as winter habitat for mule deer.

Does this mean that winter mortality operates independently of deer density? The model does not represent successional changes in vegetation resulting from effects of feeding by deer, and consequently is insensitive to an important consequence of increasing density. Successional effects operate over several years; the inferences of the model are limited to the effects of density on mortality during a single year. Within a given year, however, the model suggests mortality rates will be density independent whenever there is a low variance in the quality and/or availability of food supplies, but will be strongly influenced by density whenever those resources are variable. This is the case because under most conditions changes in food supplies or deer density must influence the quality of deer diets if those changes are to influence mortality.

In practical terms, this means that population management has the potential to reduce mortality rates on ranges with a high diversity of forages offered on topography that causes differences in the effects of snow on access to them. On ranges with low forage diversity and homogenous availability, harvest will probably fail to reduce the proportion of the population that starves. Moreover, given the relatively small impact of deer on total forage supplies (Fig. 11), it may well be that longterm successional effects also will depend on the presence of a reasonable level of variation in forage resources. It follows that estimating the average value of food re-

sources and their average biomass on the landscape is not sufficient to evaluate the quality of deer habitats or to prescribe treatments to enhance them. Instead, habitat evaluation and improvement depend on understanding the distribution relating quality and availability of deer foods to their biomass (Hobbs and Swift 1985, Hanley and Rodgers 1989).

CONCLUSIONS

Processes influencing energy intake exert a much greater impact on energy balance of mule deer during winter than processes affecting their energy expenditure. Although energy expenditure in ungulates has been investigated with great cleverness and care (*see* reviews in Hudson and White 1985*b*), controls on energy intake rarely have been studied in a way that makes them useful in predictive models. Future progress in modeling energetics of mule deer will depend on research revealing mechanisms regulating diet selection and feeding behavior, rather than merely describing their outcomes.

The predictions of the model, as well as other, more empirical results (Wickstrom et al. 1984, Spalinger et al. 1988), suggest that forage quantity will rarely influence the daily dry matter intake of mule deer. Thus, increasing forage amount will probably not improve energy balance in deer, unless those increases are accompanied by changes in the availability or nutritional value of forage. Small improvements in the condition of animals at the beginning of winter, or enhancements in forage quality that provide deer greater energy intake during winter, are likely to pay large dividends in reducing winter mortality. Reducing population size will improve animal condition and reduce mortality only when food resources are heterogenous or are exceptionally rare.

Mortality resulting from starvation is a process operating at several levels of ecological organization. Energy balance and its component processes can be represented best at the level of the individual. Variation in the impact of energy balance, as seen in its effect on mortality rates, is determined by the distribution of energy reserves among individuals and, hence, operates at the level of the population. The quantity and quality of food available to the individual is determined by the composition and productivity of plant communities and the effects of populations on them and, thus, acts at the level of the ecosystem. A thorny problem in wildlife management has been bringing information obtained at these different levels to bear on the specific, focused decisions needed to effectively manipulate animal populations and the habitats they use. The most important result of this model is the illustration that information obtained for many different reasons, in different places, using different approaches, can be assembled such that useful predictions emerge— predictions that mimic the behavior of the natural world in a reasonable way. These predictions can enhance decisions on management of mule deer.

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APPENDIX

DEER9 is a simulation model of energy balance in mule deer that predicts animal condition and starvation mortality during winter. It requires at least 256K of available RAM. A graphics card and math-co-processor are highly desirable. The model is built to allow use by persons with minimal computer experience, but the user should be familiar with DOS commands and with using prompted programs.

Obtaining the Model.—Model files can be transferred by modem over BITNET by contacting the author (NTHOBBS @ CSUGOLD). Provide your BITNET name and address, and I will respond. Alternatively, you can send me a 5.5-inch diskette and a suitable, self-addressed mailer.

Model Files.—Running the model requires only 1 file (DEER9.EXE), but others can be helpful. Source code is contained in DEER9.SRC to allow the user to modify the program. Two data files (SEVERE.DAT and MILD.DAT) were used in model experiments and provide example input for winters with high and low mortality. README.TXT contains notes on revisions, etc. A couple of files are needed to allow graphic output on monochrome monitors with Hercules cards (HGC.EXE and INIT10.COM).

Installing the Model.—Before using the model, be sure that the DOS ANSI.SYS driver is installed in your CONFIG.SYS file. See your DOS manual for instructions on setting-up this driver. If it is not installed, the model will run, but you are likely to get some strange color combinations in the screen output.

The model can be installed on a hard disk or run from the diskette drive. For hard disk users, copy the above files to the directory where you want the model and data to reside. Make that directory the default. For diskette drive users, put your working diskette (a backup copy is advisable) in a drive, and make it the default. In both cases, once the model is installed and the default drive or directory is chosen, you can begin a simulation by entering DEER9, followed by a return.

Running a Simulation.—You will need to respond to several questions to set up a simulation. Your responses can be the first letter of the appropriate word (i.e., *y* for yes) or the full word. The model is not sensitive to case; you can use capital letters or small ones. However, whenever you are

asked to enter numerical data, it is *imperative (!!!!)* that all entries include a decimal point (i.e., 10.0 rather than 10). If a simulation results in suspiciously high mortality, the first thing to check is decimal points in the input. At any time, you can exit the program by simultaneously pressing the control and break key or, if you have it, the system request key. However, *if you exit using control break while graphs are displayed, you will probably have to reboot your computer to return to a normal screen.*

Prompts for Monitor.—You will first be asked about your monitor. Respond as prompted with an *e*, *c*, or *m* followed by a return. If you have a monochrome monitor, you will be asked about your graphics card (IBM or Hercules). If you have a Hercules card, you will be given 2 prompts to enter the commands HGC FULL and INT10. VGA monitors are not supported, but probably will be in the near future.

Entering Weather Data.—At the prompt, you will first need to specify the units on weather data (English or metric). If you plan to use the input data files included on the distribution diskette, specify English units. In any case, units should not be mixed (i.e., no Celsius for temperature combined with inches for snow depth). You will be asked how you want to enter weather data—from a file (respond *f*) or from the keyboard (respond *k*). If you choose the keyboard, you will be given 3 choices for data entry (enter data, revise estimates, or leave as is). If this is your first run of the model in a session, you must respond *e* for enter data. However, if this is a repeat run, you can revise the weather input to reflect milder or more severe conditions (enter *r*). This choice was specifically designed to facilitate decisions on supplemental feeding given that you have some data for conditions observed up to the present date and some projections for what is likely to occur for the rest of the winter. Finally by choosing *l* (leave as is), it is also possible to leave the weather data unchanged and run another simulation altering other inputs. At this point, you will be prompted for information about the length of the simulation (no. of days, etc.) and then asked for daily weather input. Temperature and snow depth information should reflect the conditions deer experience as closely as possible. This is to say it would be best to get snow depth information from areas of deer concentration.

It is also possible to enter daily weather data from a data file. You will be prompted for a file name and path to its location. This file should be formatted as follows:

col	2–5:	year (e.g., 1979, integer)
col	9–10:	month (right justified integer)
col	14–15:	day (right justified integer)
col	16–25:	maximum temperature (anywhere in field, with decimal)
col	26–35:	minimum temperature (anywhere in field, with decimal)
col	36–45:	snow depth (anywhere in field, with decimal).

Units must be uniform (i.e., no mixture of English and metric). Be certain that the file is flat ASCII. This is particularly important if you use a word processor to build it. It should contain no column headings. The last day of the simulation should be March 31 (shown by a 3 in column 10 and a 31 in column 14–15). If you want to run simulations beyond March, that is acceptable; just make March 31 = 32 and the last day of the simulation = March 31. It is possible to run up to 20 years of simulations by making a contiguous data file.

Entering Habitat Data.—You will be asked if you want to change the default data that describe the food supply and the deer population. Default values are those given in Table 1. Although not all of these can be changed by the user, the major ones are available to you. If you want to change these parameters, respond *y* to the question on defaults, and a menu will appear offering you choices. Choose a parameter you wish to change and enter its number at the prompt at the bottom of the menu. A window will then open describing the parameter, its units, and default values. You can change its value in this window.

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All units must be the same as those shown in the window. If you decide you do not want to change the default value once the window has appeared, simply press the return key to get back to the menu. When you are done with changes, enter the number for exit. One other point—the code has traps for zeros that result when you press the return key alone. These traps preserve the default values and give you an easy way to return to the menu without changing a parameter. However, if you really want to enter a zero value, simply enter a number close to it (e.g., 0.000001).

Entering Data on Attributes of Deer.— You will be asked if you want to simulate a doe or a fawn. It is not possible to simulate both at once. Using a menu process identical to the one just described, you can then change default parameters describing the average animal if you wish to do so.

*Output Options.—*Respond to questions on graphics and tables. If your computer is not 100% IBM compatible, you probably cannot get graphic output and should opt for tables alone.

*Running the Simulation.—*The simulation will execute. If you do not have a math-coprocessor, it takes as long as 35 minutes/year of input data on an XT; with a coprocessor on an AT, it takes about 35 seconds.

*Printing.—*You can choose to have tables routed to your printer. If you want graphs printed, give the DOS command "graphics" before running the simulation. Then use your print screen key. Tables are printed for you if you respond *y* to the prompt.

*Repeat Simulations.—*You can run another simulation without entering new weather data, revise the data, or leave the program.